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A Method for Intravascular Injection and Bleeding of Fishes

Comparative studies of endocrinology, pharmacology, and immunology in fish would be greatly facilitated if methods were available for accurate intravascular injection and repeated blood sampling. The technique described here is simple, accurate, and safe for repeated injection and blood withdrawal via the efferent branchial artery of the gills.

Venipuncture normally is relatively easy in higher vertebrates, particularly mammals, because subcutaneous blood vessels usually are prominent enough to be readily accessible. In contrast, teleost fishes generally have no subcutaneous blood vessels large enough for injection or withdrawal of blood. The several methods for intravascular injection in use are not completely reliable. We have performed intracardiac injection repeatedly on fish, but not wholly without detrimental effects. Location of the heart for bleeding or injection requires probing with the needle while negative pressure is exerted with the syringe. This may cause considerable tissue damage, hemorrhage into the pericardial space, loss of injected material, and occasionally death secondary to pericardial tamponade. Another site for intravascular injection is the anterior segment of the dorsal aorta, which is accessible through the roof of the mouth (Schiffman, 1959). This method is unsatisfactory because of the hazards of hemorrhage and, particularly, the loss of injected material.

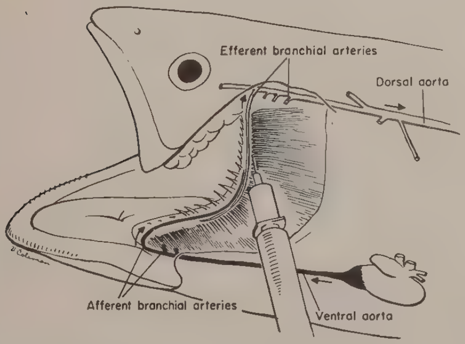

Figure 1.—Lateral view of the head region of rainbow trout showing attitude of needle in relation to branchial arch.

In recent studies on rainbow trout (*Salmo gairdneri* Richardson), we devised a method of direct intravascular injection and blood sampling which has certain advantages over those discussed above. We used the efferent section of a branchial arch, an extremely convenient and accessible site for needle puncture. In this technique the specimens are anesthetized with MS-222 (tricaine methanesulfonate).[1] The gills are exposed by lifting the operculum with the fingers of one hand while guiding the syringe with the other. The needle enters the efferent arch at a shallow angle along the longitudinal plane of the efferent section near the line of insertion of the gill filaments (Figure 1). At this location in the circulatory system the blood–gas exchange has occurred and the blood is flowing directly to the dorsal aorta.

The danger of hemorrhage is much less on the efferent side of the gill arch than on the afferent side because of the sharp fall in blood pressure between afferent and efferent (Lagler, Bardach, and Miller, 1962). The minute flow of blood which sometimes follows removal of the needle usually is stopped quickly by the mucus of the gill arches. The normal mucous layer of the gills need not be touched except at the point of needle's entry. As a precautionary measure, the needle should be guided firmly and directly into the selected arch because the tissue bearing the gill filaments tends to split longitudinally when undue leverage is applied.

A 20- or 21-gauge needle is suitable for fish that weigh one pound (454 gm) or more. Smaller specimens are difficult to bleed but injection is limited only by the size of the needle. All but the smallest fingerlings can be injected reliably. Multiple punctures may be made by alternating sides of the fish and by using other gill arches. This method of injection requires that the fish be out of water only a few seconds.

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[1] Trade names referred to in this publication do not imply endorsement of commercial products.

Our technique appears to be applicable to a broad variety of gill-bearing vertebrates. Its advantages over other methods of injection and bleeding should facilitate investigations that require intravascular injection and serial bleedings.

We wish to thank Virginia Coleman, Medical Illustrator, U. S. Fish and Wildlife Service, Seattle, Washington, for preparing Figure 1.

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A NEW SPECIES OF *PRISTIPOMOIDES* (PISCES: LUTJANIDAE) FROM THE TROPICAL WESTERN ATLANTIC

WILLIAM D. ANDERSON, Jr.

A NEW SPECIES OF *PRISTIPOMOIDES* (PISCES: LUTJANIDAE) FROM THE TROPICAL WESTERN ATLANTIC[1]

WILLIAM D. ANDERSON, JR.[2]
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ABSTRACT

A new species of lutjanid fish of the genus *Pristipomoides* is described from 28 specimens collected off Panama, Colombia, and Surinam in 137 to 183 m and one from the fish market at Bridgetown, Barbados. Brief descriptions, and discussions of synonymies and distributions of the other two western Atlantic species of the genus (*Pristipomoides aquilonaris* and *P. macrophthalmus*) are given; a key to the three species is presented.

INTRODUCTION

Twenty-eight specimens of a new species of *Pristipomoides* were collected in the western Atlantic off Panama, Colombia, and Surinam during cruises of the U. S. Bureau of Commercial Fisheries exploratory fishing vessel OREGON. An additional specimen was obtained from the fish market at Bridgetown, Barbados.

Many specimens of the other two western Atlantic species of *Pristipomoides, P. aquilonaris* (Goode & Bean, 1896), and *P. macrophthalmus* (Müller & Troschel, 1848), have been collected aboard the R/V SILVER BAY (formerly chartered by the U. S. Bureau of Commercial Fisheries) and the R/V OREGON. From this material we can derive new concepts of the biology and zoogeography of these two species.

Other species of *Pristipomoides* have been recorded from the central Pacific to the Indian Ocean. Altogether there are approximately 10 nominal species of *Pristipomoides*.

The following abbreviations are used in this paper: ANSP (The Academy of Natural Sciences of Philadelphia), BLBG (U. S. Bureau of Commercial Fisheries Biological Laboratory, Brunswick, Georgia), CNHM (Chicago Natural History Museum), FSBC (Florida State Board of Conservation, St. Petersburg), LACM (Los Angeles County Museum), MCZ (Museum of Comparative Zoology, Harvard University), SU (Stanford University), TABL (U. S. Bureau of Commercial Fisheries Tropical Atlantic Biological Laboratory, Miami, Florida), UF (Florida State Museum, University of Florida), UMML (University of Miami Marine Laboratory), UPR (Institute of Marine Biology, University of

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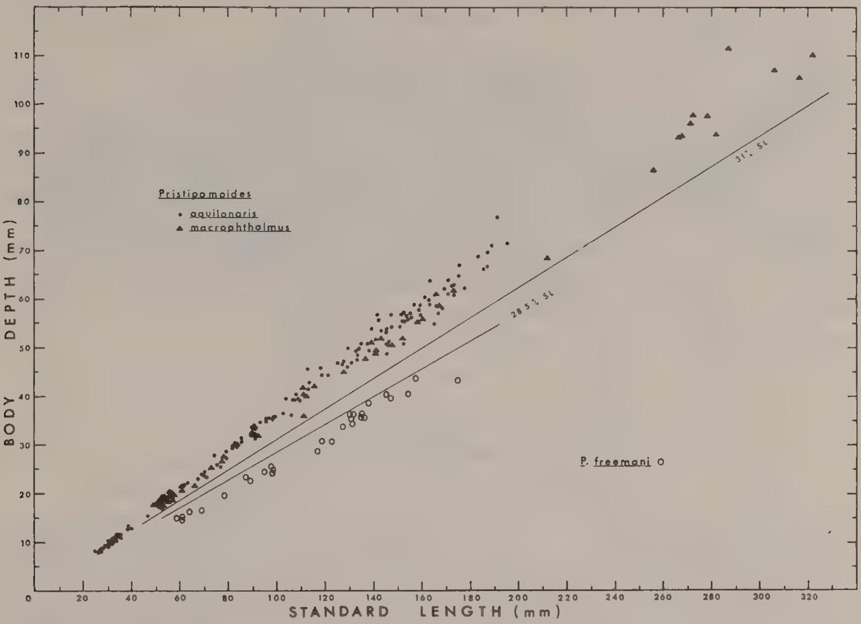

FIGURE 1. Relation of body depth to standard length for western Atlantic species of *Pristipomoides.*

Puerto Rico), and USNM (U. S. National Museum). SL designates standard length.

I am grateful to James E. Böhlke (ANSP), David K. Caldwell (LACM), Carter R. Gilbert (UF), Giles W. Mead (MCZ), Martin A. Moe, Jr. (FSBC), John E. Randall (UPR), and Leonard P. Schultz (USNM) for allowing me to examine specimens in their care; to Harvey R. Bullis, Jr. (U. S. Bureau of Commercial Fisheries, Exploratory Fishing and Gear Research Base, Pascagoula, Mississippi) for his assiduous efforts in making material available to me; to Elmer J. Gutherz (BLBG) for obtaining the specimen from Barbados; and to Grady W. Reinert (TABL) for preparing the illustration of the new species. William W. Anderson (BLBG), Frederick H. Berry (TABL), Jack W. Gehringer (BLBG), Carter R. Gilbert (UF), John E. Randall (UPR), and Loren P. Woods (CNHM) read the manuscript and made valuable comments.

METHODS

Counts and measurements were made according to the methods outlined by Hubbs & Lagler (1958), except body depth was measured from the origin of the first dorsal spine vertically to the ventral surface of the body.

On specimens in which the two pectoral fins and two pelvic fins were of unequal length, the longer fin was measured.

Pectoral-fin rays and lateral-line scales were counted on the left side of specimens, where possible.

All gillraker counts were made from the right side of the new species and in *P. macrophthalmus,* and from the right side, where possible, in *P. aquilonaris.* Both well-developed rakers and rudiments on the anterolateral surface of the anterior gill arch were included in the gillraker counts. In some specimens of *Pristipomoides aquilonaris* and *P. macrophthalmus,* "intercalated" gillrakers and rudiments may be present between, lateral to, or medial to those in the anterolateral series. These "intercalated" elements were not counted.

Counts shown in parentheses were encountered infrequently.

KEY TO WESTERN ATLANTIC SPECIES OF *Pristipomoides*

A Depth of body 3.5-4.2 times in SL (23.9-28.2 per cent SL, Fig. 1). Total number of gillrakers and rudiments on anterior gill arch 28-30(31) [(8)9(10) + (19)20-21(22)]. Lateral-line scales 50-51 .... Slender wenchman. *Pristipomoides freemani.*

AA Depth of body 2.5-3.2 times in SL (31.1-40.5 per cent SL, Fig. 1). Total number of gillrakers and rudiments on anterior gill arch 19-28 .... B

B Lateral-line scales (48)49-51(52). Total number of gillrakers and rudiments on anterior gill arch (24)25-27(28) [7-9 + (16)17-19(20)] .... Wenchman. *Pristipomoides aquilonaris.*

BB Lateral-line scales 54-56(57). Total number of gillrakers and rudiments on anterior gill arch (19)20-23(24-25) [6-7(8) + (13)14-16(17)] .... Voraz. *Pristipomoides macrophthalmus.*

Pristipomoides freemani, new species
Fig. 2

Material Examined.—HOLOTYPE: USNM 199391 (157 mm SL), from off Colombia, Lat. 12°09′N, Long. 72°47′W, 183 m, OREGON station 4913, 1 June 1964.

PARATYPES: 19 specimens, 87-154 mm SL, from same station as holotype; USNM 199387 (7, 87-154 mm SL), TABL uncatalogued (6, 90-148 mm SL), ANSP 103283 (1, 131 mm SL), CNHM 66787 (1, 136 mm SL), MCZ 44233 (1, 130 mm SL), SU 63300 (1, 134 mm SL), UF 12525 (1, 98 mm SL), and UMML 17816 (1, 97 mm SL).—Six specimens, 59-78 mm SL, off Colombia, Lat. 12°08′N, Long. 72°41′W, 137 m, OREGON station 4914, 1 June 1964; USNM 199390 (4, 59-78 mm SL) and TABL uncatalogued (2, 61-69 mm SL).—USNM 199388 (1 specimen, 116 mm SL), off Panama, Lat. 09°18′N, Long. 80°27′W,

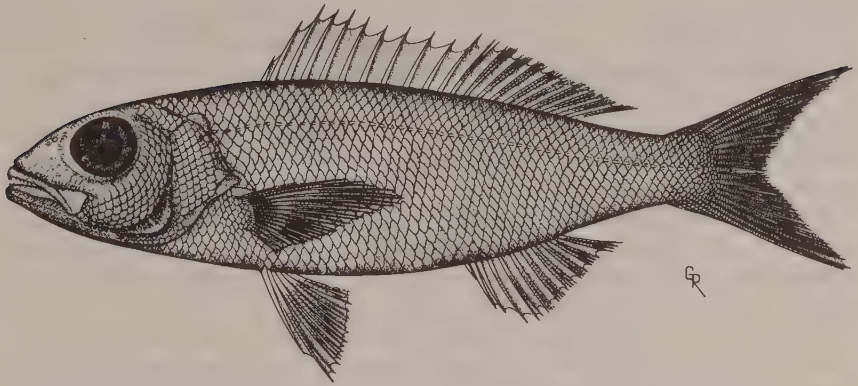

FIGURE 2. Holotype of *Pristipomoides freemani* (USNM 199391), 157 mm SL. Drawn by Grady W. Reinert.

183 m, OREGON station 3588, 29 May 1962.—USNM 199389 (1 specimen, 132 mm SL), off Surinam, Lat. 07°25′N, Long. 54°35′W, 137-146 m, OREGON station 2289, 8 September 1958. A total of 27 paratypes, 59-154 mm SL, from the western Atlantic off Panama, Colombia, and Surinam.

OTHER MATERIAL: BLBG uncatalogued (1 specimen, 175 mm SL), Barbados: Bridgetown Fish Market.

Diagnosis.—A slender species of *Pristipomoides*; depth of body 23.9-28.2 per cent SL; pectoral fin short, 21.1-27.9 per cent SL; pelvic fin short, 18.3-20.7 per cent SL; last dorsal softray short, 8.1-11.6 per cent SL; last anal softray short, 6.9-10.2 per cent SL. Total number of gillrakers and rudiments on anterior gill arch 28-31, usually 29-30, [(8)9(10) + (19)20-21(22)]. Pored lateral-line scales 50-51.

Description.—On 29 specimens (the count for holotype is followed by an asterisk): dorsal-fin rays X,11*; anal-fin rays III,8*; pectoral-fin rays 15-17 (15 in 2, 16* in 26, and 17 in 1); pelvic-fin rays I,5*; principal caudal-fin rays 17(9 + 8)*; pored lateral-line scales 50-51 (50* in 25, and 51 in 4); total number of gillrakers and rudiments on anterior gill arch 28-31, usually 29*-30, [(8)9(10) + (19)20-21(22)—upper limb 8 in 2, 9* in 24, and 10 in 3; lower limb 19 in 2, 20* in 17, 21 in 9, and 22 in 1]. In 13 specimens: vertebrae 24 (10 precaudal + 14 caudal)*.

Ranges of selected morphometric data are presented in percentage of standard length followed by the value for the holotype in parentheses. In 29 specimens (59-175 mm SL): depth of body 23.9-28.2(28.0) (Fig. 1); pectoral-fin length 21.1-27.9(27.5); pelvic-fin length 18.3-

20.7(20.1); length of last dorsal softray 8.1-11.6(ca. 10.6); length of last anal softray 6.9-10.2(ca. 10.0). In 10 specimens (59-175 mm SL): length of first dorsal spine 3.9-4.7 (broken); length of second dorsal spine 9.2-10.1(9.2); length of third dorsal spine 10.4-12.1(12.0); length of tenth dorsal spine 8.3-10.0 (broken); length of longest dorsal spine 11.3-12.7(12.0); longest dorsal spine the fourth in six specimens, the third in two, the fifth in one, the third and fourth about equally long in one; length of first dorsal softray 10.6-11.8 (broken); length of first anal spine 3.6-4.4(4.0); length of second anal spine 7.5-9.7(7.5); length of third anal spine 8.4-10.5(8.4); second anal spine shorter than third except in largest specimen, in which they are equal.

Snout usually a little shorter than horizontal diameter of fleshy orbit; interorbital flattened, least width of fleshy interorbital usually slightly less than horizontal diameter of fleshy orbit; mouth terminal, lower jaw inclined dorsally and projecting slightly beyond upper jaw when mouth is closed; maxillary ending under anterior part of eye, dorsal border of maxillary covered by a narrow suborbital bone when mouth is closed.

Upper jaw with an inner band of small, almost villiform teeth (teeth in this series are larger near anterior end of jaw), and an outer row of larger teeth with two to six (usually four) enlarged canine-like teeth near premaxillary symphysis (one to three, usually two, on either side of symphysis); no teeth at symphysis. Lower jaw with a row of canine-like teeth; at anterior end of jaw numerous smaller teeth inside the row of more widely spaced, larger canine-like teeth; no teeth at symphysis. Palatine and vomerine teeth almost villiform, except enlarged and canine-like on inner edge of vomerine patch (and on medial sides of palatine patches in some specimens); vomerine tooth patch arch-like with a blunt or rounded vertex, no backward prolongation of vomerine tooth patch on median line. Tongue without teeth.

Opercle with a prominent flat spine not extending to posterior margin of fleshy opercle; a rounded spinous projection reaching approximately to posterior edge of fleshy opercle, dorsal to opercular spine.

Preopercle without a distinct notch on vertical limb near angle; serrae on both limbs of preopercle, strongest at angle.

Snout, interorbital, preorbital, suborbital, maxillary, mandible, gular region, and branchiostegal membranes scaleless. Preopercle, interopercle, opercle, and subopercle scaled. Mid-dorsal boundary of scalation near posterior margin of orbit. An oblique band of scales on nape separated from dorsal body scales by a narrow naked area. Dorsal and anal fins scaleless.

Last softray of dorsal and anal fins produced, longer than penultimate ray. Pectoral fin usually reaches a vertical line through base of ninth or tenth dorsal spine (most often not reaching vent); pelvic fin usually reaching a vertical through base of eighth or ninth dorsal spine (short of vent). Caudal fin lunate.

Specimens in isopropanol generally straw-colored; caudal mostly straw-colored with a pale distal margin, other fins pale.

Live coloration is unknown, but a color photograph (Kodachrome) taken shortly after capture of one specimen from OREGON station 4913 showed the dorsal part of head and body to be mostly orange. Ventrolateral surfaces of head and body generally silvery. Iris pale yellow. Membrane of dorsal fin yellow distally. Pectoral-fin base pink. Pectoral, pelvic, and anal fins pale. Proximal part of caudal fin orange; most of dorsal-fin lobe yellow; most of outer part of ventral-fin lobe light pink for most of its length; pale distally; middle part of caudal fin pale. This specimen was preserved in formalin with IONOL CP-40 (40 per cent emulsifiable concentrate of butylated hydroxytoluene; see Waller & Eschmeyer, 1965:361) and later transferred to isopropanol with IONOL CP-40. About 1 year after preservation the body of this specimen was generally orange dorsally and yellowish ventrally, except for silvery ventrolateral body surface; head mainly orange dorsally, paling to light orange or yellow laterally; iris faded; proximal part of caudal fin orange to yellowish, distal part of caudal and other fins pale.

Relationships.—*Pristipomoides freemani* may be more closely related to *P. aquilonaris* than to *P. macrophthalmus*. The ranges of lateral-line scales of *P. freemani* and *P. aquilonaris* overlap and the ranges of total gillraker counts overlap slightly. *P. freemani* can readily be distinguished from both *P. aquilonaris* and *P. macrophthalmus* by its more slender body.

Distribution.—*P. freemani* has been collected off Panama, Colombia, and Surinam in 137 to 183 m. The specimen from the fish market at Bridgetown, Barbados, was presumably caught near Barbados.

Pristipomoides freemani and *P. aquilonaris* occur sympatrically in at least portions of their ranges. In addition to the specimens of *P. freemani* obtained at OREGON stations 4913 and 4914, four specimens (35-175 mm SL) of *P. aquilonaris* were collected at 4913 and five specimens (54-168 mm SL) at 4914. Twenty-two specimens (80-165 mm SL) of the related species *Etelis oculatus* (Valenciennes, 1828) were also collected at OREGON station 4913.

Etymology.—This species is named for Harry W. Freeman, College of Charleston, Charleston, South Carolina, who first introduced me to the study of fishes.

Pristipomoides aquilonaris (Goode & Bean)

Anthias aquilonaris Goode & Bean, 1896: 238 (Gulf of Mexico).

[?] *Etelides aquilionaris,* Jordan & Thompson, 1905: 241 (Gulf Stream, toward the Carolina coast).

[?] *Pristipomoides macrophthalmus* (*non* Müller & Troschel), Hildebrand, *in* Longley & Hildebrand, 1941: 122 (Tortugas).

Pristipomoides andersoni Ginsburg, 1952: 91 (several Gulf of Mexico localities).

Material Examined.—156 specimens (25-195 mm SL), including the holotypes of *Anthias aquilonaris* (USNM 37346) and *Pristipomoides andersoni* (USNM 151882), and 18 paratypes of *P. andersoni* (USNM); specimens from Puerto Rico: off Añasco (UPR 2358) and Córcega (UPR 293); off Louisiana (Lat. 29°09.8′N, Long. 88°36′W; FSBC 1609); from SILVER BAY stations 301, 327, 1268, 1359, 2354, 2398, 2411, 2930, 3957, 5161, 5389, 5390, 5491, 5493 (BLBG in part), 5717, and 5742; and from OREGON stations 944 (UF 3641), 1060 (UF 12315), 1356 (BLBG in part), 1590 (UF 731), 1995, 2203, 2274, 3548, 3587, 3590, 3595, 3623, 3931, 4083, 4151, 4165, 4184, 4191, 4192, 4198, 4200, 4391, 4393, 4394, 4465, 4471, 4575, 4628, 4696, 4846, 4913, 4914, and 5032. (Where no collection is given for a station number, specimens are deposited at TABL.)

Description.—Dorsal-fin rays X,(10)11 (10 softrays in one specimen, 11 in 52, and 8 in one with a damaged fin). Anal fin rays III, 8 (8 softrays in 52 specimens; 7 in two specimens in which radiographs show the usual number of pterygiophores, but with one ray undeveloped). Pectoral-fin rays 15-17, 14 on the right side of the holotype of *P. aquilonaris* (54 specimens; 15 in 26, 16 in 27, and 17 in 1). Pelvic-fin rays I,5 (46 specimens). Principal caudal-fin rays 17 (9+8; 50 specimens). Vertebrae 24 (10 precaudal + 14 caudal; 20 specimens). Pored lateral-line scales 48-52 (128 specimens; 48 in 1, 49 in 10, 50 in 102, 51 in 13, and 52 in 2). Total number of gillrakers and rudiments on anterior gill arch 24-28, usually 25-27, [7-9 + (16)17-19(20)—124 specimens: upper limb 7 in 13, 8 in 81, and 9 in 30; lower limb 16 in 1, 17 in 37, 18 in 68, 19 in 15, and 20 in 3].

Selected morphometric data are presented. Variation with size is indicated in parentheses. The body is deeper than that of *P. freemani* (see Fig. 1), 31.1-40.5 per cent SL in 156 specimens of 25-195 mm SL (31.1-34.7 per cent SL in 42 specimens of 25-53 mm SL, 33.0-40.5 per cent SL in 114 specimens of 61-195 mm SL). Pectoral fin 20.2-34.5 per cent SL in 45 specimens of 34-195 mm SL (20.2-26.0 per cent SL in four specimens of 34-53 mm SL, 29.3-34.5 per cent SL in 41 specimens of 63-195 mm SL). Pelvic fin 19.4-27.2 per cent SL in 46 specimens of 34-195 mm SL (19.4-21.7 per cent SL in four specimens of 34-53 mm SL, 22.1-27.2 per cent SL in 42 specimens of 61-195 mm SL). Length of last dorsal softray 10.1-16.0 in 34 specimens of 34-195 mm SL (10.1-12.7 per cent SL in seven specimens of 34-80 mm SL, 12.5-16.0 per cent SL in 27 specimens of 83-195 mm SL). Length of last anal softray 9.2-16.0 per cent SL in 39 specimens of 34-195 mm SL (9.2-11.0 per cent SL in four specimens of 34-53 mm SL, 11.0-16.0 per cent SL in 35 specimens of 61-195 mm SL).

Synonymy.—Pristipomoides aquilonaris was originally described by Goode & Bean (1896:238). They stated that, "A specimen (Cat. No. 37346, U.S.N.M.) obtained by the FISH HAWK, has been misplaced, and cannot now be fully described. The name *Anthias aquilonaris* has been proposed by us for it. It is allied to *Anthias oculatus*, C & V."

At the U. S. National Museum I found a specimen with the catalogue number (37346) mentioned by Goode & Bean, but the data with the specimen had an ALBATROSS station number (2402). Jordan and Evermann (1898:1283) gave the collection data as: "Gulf of Mexico, Lat. 28°36′N. Long. 85°33′30″W." This is the position of ALBATROSS station 2402 (additional pertinent data for this station are 111 fathoms and 14 March 1885). Goode & Bean apparently erroneously recorded an ALBATROSS specimen as being collected by the FISH HAWK.

Although Goode & Bean (1896:238) stated that their specimen of *Anthias aquilonaris* could not "now be fully described," they did give the following data: "A note [by whom?] indicates that the length of its head was equal to the height of its body, which is contained 2⅚ times in the total length (without caudal). The diameter of the orbit is contained 3⅙ times in the head. The maxillary bone was naked, rather than scaled as in *A. oculatus;* and the scales number 53 in the lateral line, 7 above and 14 below. The radial formula was D.X,11;A.III,8." Proportions of body parts calculated from my measurements agree closely with those of Goode & Bean, and my counts of dorsal- and anal-fin rays are identical with theirs. My count of lateral-line scales (50 on each side) and number of scales above (ca. 8) and below (ca. 15) the lateral line differ from theirs. These differences can be attributed to differences in methods of counting. Goode & Bean's specimen was 9 inches (229 mm). The total length of the specimen (USNM 37346) is about 230 mm or approximately 9 inches.

Goode & Bean (1896:238) mentioned a small specimen (less than 2 inches [51 mm]) collected by the BLAKE off Dominica in 524 fathoms (958 m) which they suggested might possibly belong to *aquilonaris.* I examined a specimen (MCZ 27948), 47 mm SL, labeled as *Anthias aquilonaris,* which was collected by the BLAKE off Dominica. Both the MCZ catalogue and the data with the specimen give the depth as 524 fathoms, but this seems much too deep for a lutjanid. Although the specimen is in only fair condition, it is easily determined that it is not a *Pristipomoides*; the maxillary has scales, whereas *Pristipomoides* lacks such scales.

Jordan & Thompson (1905:241-242) described and figured a specimen (length 1.87 inches [47 mm]) obtained "in the Gulf Stream toward the Carolina coast" and ascribed it to *Anthias aquilonaris* for which they erected the genus *Etelides*. Their description and figure resemble *P. aquilonaris,* but the description differs from *P. aquilonaris* in that the "preopercle [has] both limbs entire" and "dorsal [is] deeply notched." Jordan & Thompson's *Etelides aquilionaris* may be conspecific with *P. aquilonaris,* but this cannot be ascertained until their specimen is located.

Ginsburg (1952:91) placed the reference to *P. macrophthalmus* by Hildebrand (*in* Longley & Hildebrand, 1941:122) in synonymy of his new species, *P. andersoni.* I have examined seven paratypes of *P. andersoni* from Tortugas, one of which has a Carnegie Institution of Washington accession number, suggesting that at least one and possibly all 33 specimens mentioned by Hildebrand were *P. aquilonaris.*

Ginsburg (1952:91-93) probably did not refer to the holotype of *P. aquilonaris* when he described *P. andersoni.* I have very carefully compared the holotypes of *P. aquilonaris* (USNM 37346) and *P. andersoni* (USNM 151882), and found that they are conspecific.

Distribution.—P. aquilonaris is a wide-ranging species, but has previously been reported only from the Gulf of Mexico (Ginsburg, 1952:92; Briggs, 1958:279). I examined specimens from the western Atlantic, the Straits of Florida, Gulf of Mexico, and Caribbean Sea (*i.e.,* off North Carolina, South Carolina, Georgia, the Atlantic coast of Florida, Tortugas, the Gulf coast of Florida, Alabama, Mississippi, Louisiana, Texas, Mexico [Tamaulipas, Tabasco, and Yucatán], Jamaica, Hispaniola, Puerto Rico, Honduras, Panama, Colombia, Venezuela, Tobago, British Guiana, Surinam, and French Guiana). The species probably occurs off many of the other islands of the Antilles, all Mexican states bordering the Gulf of Campeche, and most of the Caribbean coast of Mexico and Central America.

Ginsburg (1952:92) gave the depth range for this species as 13 to 95 fathoms (24-174 m). I examined specimens from 22 to 200 fathoms (40-366 m). At a longline station (OREGON 1590) over a depth of 900 fathoms (1646 m), 13 specimens (25-34 mm SL) of *P. aquilonaris* were regurgitated by a "dolphin" (*Coryphaena*?). Twenty-four other specimens (28-39 mm SL) of *P. aquilonaris*, labeled as being from OREGON station 1356, a longline station over 950 fathoms, may have been inadvertently mislabeled or may have been regurgitated by some larger fish caught at that station.

Two specimens (171-186 mm SL) of *P. aquilonaris* were caught with two (112-115 mm SL) specimens of *P. macrophthalmus* at SILVER BAY station 5161 (Lat. 19°57.5′N, Long. 71°05′W, 150-190 fathoms [274-347 m]; 14 October 1963) off Hispaniola.

Pristipomoides macrophthalmus (Müller & Troschel)

Centropristes macrophthalmus Müller & Troschel, *in* Schomburgk, 1848: 666 (Barbados).

Anthias macrophthalmus, Günther, 1859: 91 (Caribbean Sea).

Mesoprion vorax Poey, 1860: 151 (Cuba).—Poey, 1861: 365 (reference).

Platyinius vorax, Gill, 1862: 236 (new genus).—Poey, 1868: 292 (reference).—Poey, 1875: 31 (reference). Jordan, Evermann, & Tanaka, 1927: 667 (*vorax = macrophthalmus*).

[?] *Elastoma macrophthalmum,* Cope, 1871: 468 (St. Kitts).

Aprion macrophthalmus, Jordan & Swain, 1884: 467 (description). Jordan & Fesler, 1893: 456 (description). Jordan & Evermann, 1898: 1280 (description).

Pristipomoides macrophthalmus, Jordan & Thompson, 1911: 459 (*Platyinius* Gill = *Pristipomoides* Bleeker; *vorax = macrophthalmus*). Jordan & Jordan, 1922: 48 (reference). Jordan, Evermann, & Clark, 1930: 328 (compiled).

Material Examined.—68 specimens (49-322 mm SL), including the holotype of *Mesoprion vorax* (MCZ 26479); specimens from Jamaica: near Port Antonio (LACM 6133); Puerto Rico: 5-6 miles south of La Parguera (TABL; UPR 2516); from SILVER BAY stations 2417, 2464, 2467 (BLBG in part), 2470, 2471, 2472, 2477, 2479, 3498, 3499 (BLBG in part), 3512 (ANSP 101996), 5161, 5167, and 5193; and from OREGON stations 3549 (LACM 6263), 3567, and 3585. (Where no collection is given for a station number, specimens are deposited at TABL.)

Description.—Dorsal-fin rays X,11 (11 softrays on 38 specimens, 7 in one with damaged fin). Anal-fin rays III,8 (39 specimens). Pectoral-fin rays 15-16 (39 specimens; 15 in two and 16 in 37). Pelvic-fin rays I,5 (34 specimens; 4 softrays on the right side of one specimen). Principal caudal-fin rays 17 (9+8; 38 specimens). Vertebrae 24 (10 precaudal + 14 caudal; 13 specimens). Pored lateral-line scales 54-57 (67 specimens; 54 in 8, 55 in 46, 56 in 12, and 57 in 1). Total number of gillrakers and rudiments on anterior gill arch 19-25, usually 20-23 [6-7(8) + (13)14-16(17)—68 specimens: upper limb 6 in 8, 7 in 56, and 8 in 4; lower limb 13 in 3, 14 in 27, 15 in 24, 16 in 13, and 17 in 1].

Selected morphometric data are presented below. Variation with size is indicated for some characters in parentheses. The body is deeper than that of *P. freemani* (about as deep as that of *P. aquilonaris*; see Fig. 1) 32.3-38.8 per cent SL in 67 specimens of 49-322 mm SL. Pectoral fin 29.1-35.1 per cent SL in 32 specimens of 50-322 mm SL. Pelvic fin 18.7-24.4 per cent SL in 30 specimens of 50-322 mm SL (18.7-20.5 per cent SL in seven specimens of 50-84 mm SL, 20.9-24.4 per cent SL in 23 specimens of 90-322 mm SL). Length of last dorsal softray 9.3-16.3 per cent SL in 20 specimens of 57-322 mm SL (9.3-11.9 per cent SL in 3 specimens of 57-73 mm SL, 12.6-16.3 per cent SL in 17 specimens of

84-322 mm SL). Length of last anal softray 10.4-15.3 per cent SL in 18 specimens of 57-322 mm SL (10.4-12.8 per cent SL in 6 specimens of 57-92 mm SL, 12.0-15.3 per cent SL in 12 specimens of 112-322 mm SL).

Synonymy.—Müller & Troschel described *Pristipomoides macrophthalmus* from a 1-inch specimen. Their description omits clearly diagnostic characters, but it could conceivably represent a *Pristipomoides*. My examination of the holotype of *Mesoprion vorax* (MCZ 26479), generally considered to be a junior synonym of *P. macrophthalmus,* indicates that it has the characters (low gillraker count and high lateral-line scale count) used by Ginsberg to discriminate *macrophthalmus* from *andersoni* (=*aquilonaris*) and which can be used to separate *macrophthalmus* from *aquilonaris* and *freemani*. The status of Müller & Troschel's species cannot definitely be established until the holotype, if extant, is examined. Considering the meager data now available and in the interests of nomenclatural stability, I regard Müller & Troschel's description as representing the species herein designated as *macrophthalmus.*

Distribution.—*P. macrophthalmus* has a much more restricted range than *P. aquilonaris.* Jordan, Evermann, & Clark (1930:328) reported it from "West Indies, Habana," and Cervigón (1963:123) reported it off Venezuela as far south as Boca Grande del Orinoco. I examined specimens from the Straits of Florida, and off the Bahamas, Cuba, Jamaica, Hispaniola, Puerto Rico, Nicaragua, and Panama from depths of about 60 to 300 fathoms (110-549 m). Cervigón (1963:123) gave a depth range of 25 to 70 fathoms (46-128 m) for this species. The specimens collected at OREGON stations off Nicaragua (station 3567) and Panama (station 3585) appear to be the first reported off the mainland of Central America. *P. macrophthlamus* very likely occurs off most of the islands in the West Indies, and possibly off much of the Caribbean coast of Central America.

As mentioned under the discussion of distribution of *P. aquilonaris, P. macrophthalmus* was caught with *P. aquilonaris* at one station (SILVER BAY 5161, off Hispaniola). Since there is considerable geographic and bathymetric overlap in the ranges of these two species, they likely occur together at other places; indeed they may even be syntopic (see Rivas, 1964:42-43). All three western Atlantic species of *Pristipomoides* may occur together in the Lesser Antilles.

SUMARIO

UNA NUEVA ESPECIE DE *Pristipomoides* (PISCES: LUTJANIDAE) DEL ATLÁNTICO OCCIDENTAL TROPICAL

Se describe una nueva especie, *Pristipomoides freemani,* basándose en 28 ejemplares cogidos frente a Panamá, Colombia y Surinam, en unas 75 a 100 brazas (137 a 183 m) de profundidad y uno del mercado de peces en Bridgetown, Barbados. Se dan breves descripciones y discusiones

de la sinonimia y distribución de las otras dos especies del Atlántico Occidental de *Pristimoides* (*P. aquilonaris* y *P. macrophthalmus*). Se presenta una clave para las tres especies del Atlántico Occidental.

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NOTE ADDED IN PROOF

Since the manuscript was submitted, I have received on loan two specimens of *Pristipomoides* from Fernando Cervigón (Estacion de Investigaciones Marinas de Margarita, Punta de Piedras, Nueva Esparta, Venezuela).

One of these is a specimen (159 mm SL) of *P. freemani* (Museo de Historia Natural La Salle [MHNLS] cat. no. 1926) collected off Higuerote (Estado Miranda), Venezuela, in less than 70 fathoms (128 m) by Agustín Fernandez Yepes in September 1965. This is the first record of *P. freemani* from off Venezuela.

The other is a specimen (ca. 233 mm SL) of *P. aquilonaris* (MHNLS cat. no. 802) collected east of Los Hermanos, Venezuela, in 60 to 120 fathoms (110-219 m) by Fernando Cervigón on 5 October 1965. This is the largest specimen of *P. aquilonaris* that I have seen.

Family Synodontidae

Lizardfishes

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Characters.[1] BODY slender and cylindrical or slightly compressed. HEAD depressed to compressed; bone surfaces of top of head little to very rugose. EYE of moderate size and laterally directed. ADIPOSE EYELID on anterior and posterior margins of eye. PUPIL rounded. INTERORBITALS of moderate size. NOSTRILS double and oval, the anterior one with a dermal flap on its posterior margin. MOUTH large; gape tending to be oblique. UPPER JAW not protractile, bordered its entire length by the premaxillary, its length more than half the length of head and extending well past posterior margin of orbit in adult specimens; upper jaw not arched at symphysis; maxillary rudimentary and closely adherent to premaxillary; no supramaxillary bone. LOWER JAW terminal or included, with or without a fleshy knob at its tip. TONGUE well developed, free at tip, and supported by a well developed glossohyal. TEETH of moderate size, usually cardiform and depressible, not barbed; no distinct canines; teeth in bands around both jaws, in one or two series on palatines, present on tongue and sometimes on vomer. VOMER present or absent. GILL OPENINGS large. GILL MEMBRANES free from isthmus. GILL ARCHES 4, extending far forward into mouth, well in advance of the angle of gape. OPERCULAR FLAP with free edge formed by both the opercle and the subopercle. GILL RAKERS rudimentary or minute and spine-like. PSEUDOBRANCHIAE well developed. BRANCHIOSTEGALS about 11–18. ALIMENTARY CANAL short. PYLORIC CAECA numerous. SWIM BLADDER small or absent. SCALES cycloid, small to large, covering the body, cheeks, and opercles; top of head naked; enlarged or modified scales at bases of caudal, dorsal, pelvic, and pectoral fins. LATERAL LINE nearly straight and terminating at bases of midcaudal rays, the pored scales not enlarged. LUMINOUS ORGANS absent. FINS with articulated soft rays excepting a few anterior secondary caudal rays; none greatly prolonged except the elongated anterior dorsal fin rays reported for one species, *Saurida tumbil* (Bloch) (*54*: 25, figs. 2, 3); no detached fin rays. DORSAL fin about midway on back, posterior to pelvic insertion; the first 2 rays always unbranched, the others usually branched, the last ray always branched to its base. ANAL fin posterior to end of dorsal fin; the first 2 rays always unbranched, the other rays branched or unbranched, the last ray always branched to its base. DORSAL ADIPOSE fin over base of anal fin [apparently missing in adults of an Australian species, *Xystodus sageneus* (Waite) (*75*: 173)]. PECTORAL fins inserted about on midline of body close to head, not reaching to, or extending beyond, pelvic origin; the first and last rays always unbranched, the other rays usually branched. PELVIC fins with 8 or 9 rays, the fins close together and inserted abdominally, posterior to pectoral origin and anterior to dorsal origin; the first and last rays unbranched, all other rays branched; the rays varying from about equal in length to last rays much longer than first rays. CAUDAL fin forked, 9 + 10 principal rays, the most dorsal and most ventral ray each unbranched, the others branched. ANUS located just anterior to anal fin origin.

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[1] Our examination of specimens has been confined almost entirely to species occurring in the Atlantic Ocean. Although we have recognized convincing published criteria concerning Indo-Pacific species, some of the family and generic characters we use have evolved from our examination of specimens from the Atlantic. A revision of Indo-Pacific species may produce a partial alteration or expansion of these characters.

Developmental Stages. Synodontids undergo a form of early development that might best be termed a metamorphosis. Until fin rays and scales can be counted, it is difficult to identify the larvae with a species, or even genus. Norman (*60*: 100, fig. 1) in 1935 summed up the meager information available on larval stages. Subsequent to this, *Trachinocephalus myops* (Forster) postlarvae were identified by Gopinath (*30*: 11, fig. 1) from a series of specimens 27 to 35 mm TL, and Hollister (*37*: 387, figs. 1–4) gave information on development of the caudal osteology of specimens 29 and 39 mm SL and larger. For the genus *Synodus*, Breder (*12*: 13, pls. 1, 2, fig. 1) described growth and transformation of a specimen of *S. foetens* (Linnaeus), initially about 25 mm SL, that was kept in an aquarium, and Hollister (*37*: 391, figs. 5–18) gave details of de-

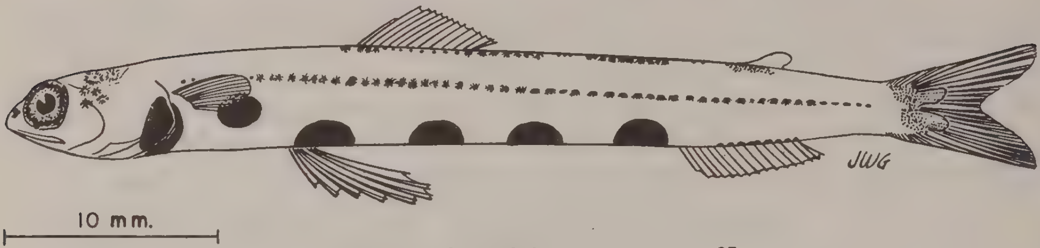

Figure 8. *Trachinocephalus myops*, 42.5 mm SL.

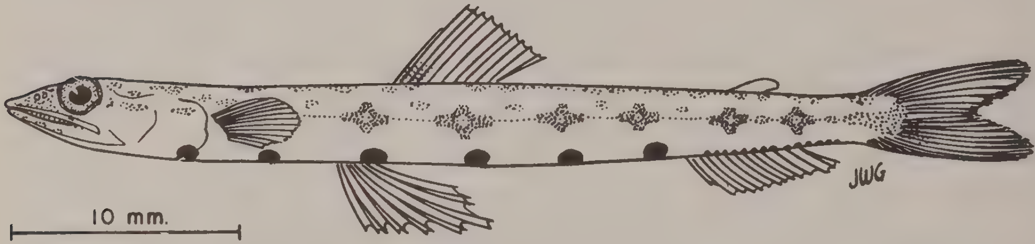

Figure 9. *Synodus foetens*, 40.0 mm SL.

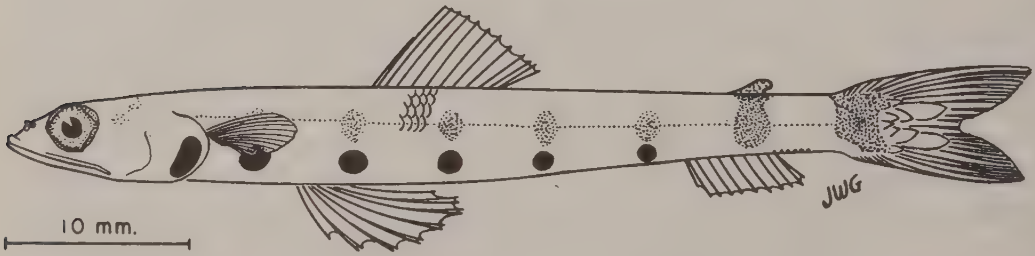

Figure 10. *Synodus saurus*, 46.0 mm SL.

velopment of the caudal osteology of specimens 28 mm SL and larger; Nichols and Murphy (*59*: 235) briefly contrasted specimens of *S. foetens* and *S. scituliceps* Jordan and Gilbert of about 39 mm SL; and Gopinath (*30*: 11, fig. 2) identified postlarval stages of 30 to 32 mm TL as *S. indicus* (Day). For the genus *Saurida*, Gopinath (*30*: 12) described postlarval stages of 25 to 37 mm TL, identified as *Saurida tumbil*; and Nair (*58*: 197) described eggs and embryos thought to belong to this species. [Recently, Gibbs[2] has published accounts of postlarvae of the following species: *Trachinocephalus*

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[2] Gibbs Jr., R. H., A synopsis of the postlarvae of western Atlantic lizard-fishes (Synodontidae), Copeia, 1959: 232–236, 2 figs.

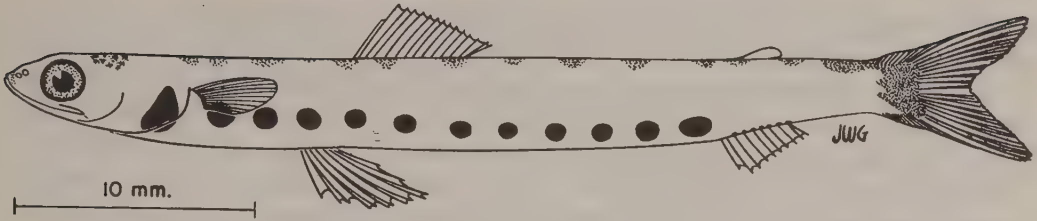

FIGURE 11. *Synodus synodus*, 37.0 mm SL.

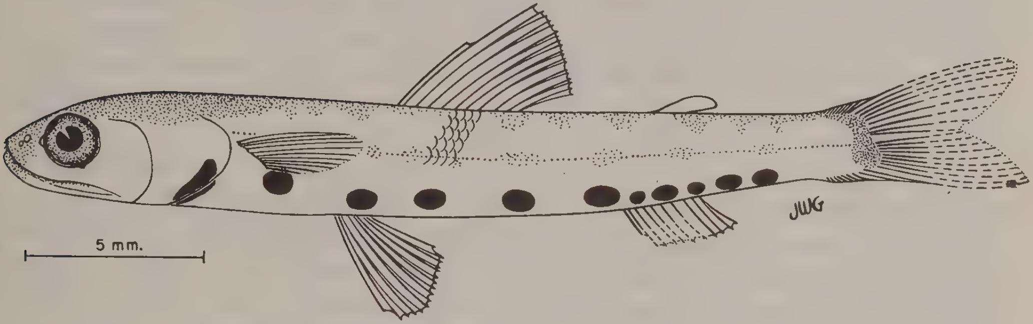

FIGURE 12. *Saurida brasiliensis*, 25.0 mm SL.

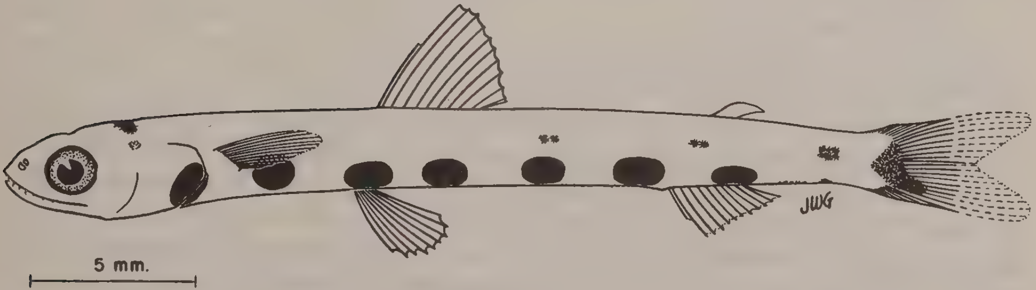

FIGURE 13. *Saurida suspicio*, 27.0 mm SL.

myops; *Synodus foetens*, *S. saurus*, *S. poeyi* and *S. synodus*; *Saurida brasiliensis*, *S. normani*, and *S. suspicio*.]

There is insufficient material for a comprehensive presentation of the larvae, but we illustrate those larvae or postlarvae that are available and to which we can apply a name. Especially significant in larval identification are the paired spots or patches of dark pigment in the lining of the peritoneum and along the midventral line at the anal fin and caudal peduncle. Because of their intraspecific consistency, the number, position, and size of these spots are of great aid in identifying small fish—once the pattern is established for the species from specimens having sufficient adult characters to allow specific identification. Transmitted light is usually sufficient to reveal the position and number of spots on translucent larvae, but in small fish that have begun to develop pigment and thickness to the body, the pattern is lost in the tissue. On such small opaque specimens the spots stand out sharply when the fish are cleared and stained with alizarine red, as the clearing solution does not appreciably affect the pigment in these spots. The size at which the pigment spots are no longer present, or discernible, has not been determined. It has been possible to determine the pattern of pigment spots for all species except *Saurida normani* Longley, for which we have no small specimens.

Trachinocephalus myops (Forster). Fig. 8. Specimen 42.5 mm SL, with 6 large preanal pairs of pigment spots, from the western Caribbean Sea, OREGON St. 1863, 16°22′N, 83°31′W, August 20, 1957, BLBG collections.

Synodus foetens (Linnaeus). Fig. 9. Specimen 40.0 mm SL, with 6 preanal pairs of pigment spots, from St. Simons' beach, Georgia, April 13, 1956, BLBG collections.

Synodus saurus (Linnaeus). Fig. 10. Specimen 46.0 mm SL, 6 preanal pairs of pigment spots, from north shore of Hog I., Bahamas, April 14, 1955, ANSP 74963.

Synodus synodus (Linnaeus). Fig. 11. Specimen 37.0 mm SL, with 12 or 13 preanal pairs of spots, from near the 100-fathom line off Cape Lookout, North Carolina, THEODORE N. GILL cruise 2, Regular St. 71, 34°04′N, 76°15′W, May 9, 1953, BLBG collections. As this species has not been recorded from inshore waters of the United States, but does occur in the Bahamas, we assume that this specimen had drifted northward in the Gulf Stream.

Saurida brasiliensis Norman. Fig. 12. Specimen 25.0 mm SL, with 6 preanal pairs of pigment spots plus several pairs at anal fin and on caudal peduncle, from the Campeche Banks, lower Gulf of Mexico, August 27, 1951, CNHM 64305.

Saurida suspicio Breder. Fig. 13. Specimen 27.0 mm SL, with 6 preanal pairs of pigment spots plus one pair at anal fin, from the Campeche Banks, lower Gulf of Mexico, December 6, 1952, CNHM 64306. The dorsal, anal, and pectoral ray counts fall within the ranges for *S. suspicio*, *S. caribbaea*, and *S. brasiliensis*. However, the pattern of paired pigment spots matches that in a larger stained specimen of *S. suspicio* 39.5 mm (Fig. 33) while differing from the patterns for *S. brasiliensis* (Fig. 12) and a stained 55-mm specimen of *S. caribbaea* (6 preanal pairs plus several at anal fin and behind).

S. normani. We have no small specimens and were unable to determine the pigment pattern for this species.

Saurida caribbaea and *S. brasiliensis.* The pigment patterns for these species are similar (6 preanal pairs plus several at anal fin and behind), and because there is overlap in ranges of dorsal, anal, and pectoral rays, we conclude it would be difficult, if not impossible, to distinguish between the larvae of these two species prior to formation of lateral-line scales.

Synodus poeyi Jordan or *S. intermedius* (Spix). We had no larvae identifiable as *S. poeyi* or *intermedius.* However, we were able to determine the pattern of pigment spots by staining juveniles, 50 and 49.5 mm, respectively, which still retained the spots.

The patterns were identical (6 preanal pairs), and similar to that for *S. foetens* (Fig. 9). We conclude that, with the overlap in ranges of dorsal, anal, and pectoral rays, and scale counts, it would be difficult if not impossible to distinguish between the larvae of these prior to the development in *S. poeyi* of the longer anterior dorsal rays and fleshy knob on the mandible tip, and in *S. intermedius* of the shoulder spot. The overlap in ranges of ray counts for *S. saurus* with those for *S. foetens*, *S. poeyi*, and *S. intermedius* would prove a problem in separation of some of the larvae of these species, since their pigment patterns are similar and since the adults are separated in part on the basis of numbers of lateral-line scales and rows of scales between the lateral line and the base of the dorsal fin, neither of which character is present in larvae.

Remarks. In 1862 Gill (*26*: 53) established a new family name, Synodontoidae, and a new subfamily name, Synodontinae, for the genera *Synodus* and *Trachinocephalus*. In later publications Gill (*27*: 810) amended the spelling of the family name to Synodontidae. A substitute family name, Synodidae, is incorrect and has been little used (*62*: 1; *13*).

The genera *Harpadon* LeSueur 1825, *Bathysaurus* Günther 1878, and *Bathymicrops* Murray and Hjort 1912, included in the family Synodontidae by some recent authors, are excluded. These genera are placed in the families Harpadontidae, Bathysauridae (p. 103), and Ipnopidae (p. 147), respectively.

Genera. In the family, as presently constituted, four genera are recognized: *Synodus* Gronow 1763, *Saurida* Valenciennes 1849, and *Trachinocephalus* Gill 1861, each occurring in the Atlantic, Pacific, and Indian oceans; and *Xystodus* Ogilby 1910, which has been recorded only from Australia.

Whitley (*77*: 173) pointed out errors in the original description of *Xystodus banfieldi* Ogilby (*62*: 6), placed *X. banfieldi* in the synonymy of *Synodus sageneus* Waite, and assigned *S. sageneus* to the genus *Xystodus*. Waite (*75*: 58, pl. 8, fig. 1) indicated that his type (and only specimen) of *Synodus sageneus* had no adipose fin, but a pit was present which suggested its position. Whitley said of *X. sageneus*: "Small examples have a minute adipose dorsal fin, but this is lost and its site covered by scales in larger fish." Other than the reported absence of an adipose fin in large specimens of *Xystodus sageneus* (Waite), these fish could well fit in the genus *Synodus*, and it is our opinion that a separate genus is not justified.

Methods and Definitions. The meristic counts and the measurements from which proportional values were determined as follows:

STANDARD LENGTH: tip of snout to base of caudal fin.

BODY DEPTH AND WIDTH: measured at base of pelvic fin.

HEAD LENGTH: distance between perpendiculars to sagittal plane of body at tip of snout and posterior extension of fleshy margin of opercle.

SNOUT LENGTH: distance between perpendiculars to sagittal plane of body at tip of snout and anterior margin of orbit.

EYE DIAMETER: horizontal measure.

INTERORBITAL: width of bony interorbital at narrowest point.

PREMAXILLARY: straight line distance along upper jaw between perpendiculars to sagittal plane of body at tip of snout and posterior end of premaxillary.

DISTANCE FROM SNOUT TO ORIGIN OF PELVIC, DORSAL, AND ANAL FINS: distance between perpendiculars to sagittal plane of body at tip of snout and origin of fin (insertion of first ray).

DISTANCE FROM ORIGIN OF DORSAL FIN TO ORIGIN OF ADIPOSE FIN: distance between perpendiculars to sagittal plane of body at origin of dorsal fin and origin of adipose fin.

DISTANCE FROM TIP OF PECTORAL FIN TO ORIGIN OF PELVIC FIN: with pectoral fin laid back against side of body, the distance between perpendiculars at tip of pectoral fin and origin of pelvic fin; a minus (−) value if the pectoral tip falls short of origin of pelvic, and a plus (+) value if the pectoral tip exceeds origin of pelvic.

LENGTH OF FIRST PELVIC RAY, LONGEST PELVIC RAY, LONGEST PECTORAL RAY, LONGEST DORSAL RAY, AND LAST DORSAL RAY: distance from tip of ray to ray base (insertion).

LENGTH OF DORSAL AND ANAL BASES: distance between perpendiculars to sagittal plane of body at origin of fin (insertion of first ray) and terminus of fin base (insertion of last ray).

PREDORSAL SCALES: number of scales bisected by a straight line between occiput and origin of dorsal fin; irregular placement of scales causes this count to be quite variable in some species.

ROWS OF COMPLETE SCALES BETWEEN LATERAL LINE AND BASE OF DORSAL FIN: number of rows of complete scales, not including modified scales along all or part of dorsal fin base of some species (counted as one-half scales by some authors).

SCALES IN LATERAL LINE: number of modified scales between operculum and base of caudal fin; several scales extending onto caudal fin not included.

DORSAL AND ANAL RAYS: total number, including simple and branched rays—the last ray, divided to its base, counted as one ray.

PECTORAL AND PELVIC RAYS: total number, including simple and branched rays.

Key to Atlantic Genera

1a. Pelvic rays 8; inner rays of pelvic fins much longer than outer ones; a single band of teeth on each side of palate; vomer absent.

  2a. Anal fin origin about midway between base of caudal fin and insertion of pectoral fin; anal fin origin closer to origin of pelvic fin than to base of caudal fin; anal fin base more than 23 % of SL; anal rays 14–16. *Trachinocephalus* Gill 1862, p. 37.

  2b. Anal fin origin much nearer to base of caudal fin than to insertion of pectoral fin; anal fin origin closer to base of caudal fin than to origin of pelvic fin; anal fin base less than 18 % of SL; anal rays 8–13 (rarely 14 in *Synodus foetens* only). *Synodus* Gronow 1763, p. 46.

1 b. Pelvic rays 9; inner rays of pelvic fins about equal to, or not much longer than, outer ones; a double band of teeth on each side of palate; vomer present, frequently toothed. *Saurida* Valenciennes 1849, p. 84.

Genus *Trachinocephalus* Gill 1862

Lizardfish, Snakefish

Trachinocephalus Gill, Cat. Fishes E. Coast. U.S., Proc. Acad. nat. Sci. Philad. (1861), Addend., 1862: 53; type species by monotypy, *Salmo myops* Forster *in* Bloch and Schneider, 1801.

Generic Synonym:

Goodella Ogilby, Proc. Linn. Soc. N.S.W., *22* (2), 1897: 250; type species by monotypy, *Goodella hypozona* Ogilby, 1897.

Characters. BODY slender and slightly compressed laterally; depth at origin of pelvic fins greater than width. HEAD compressed; bone surfaces on top of head very rugose. EYE with a narrow adipose eyelid on its anterior and posterior margins. INTERORBITAL space deeply concave. SNOUT blunt and very short, its length always shorter than eye diameter. LOWER JAW usually extending beyond upper jaw when the mouth is closed; no fleshy knob at tip. TEETH in the upper jaw large, compressed, and pointed, forming a narrow band, with the inner ones larger and depressible; a band of similar teeth in lower jaw, with the inner ones larger and depressible, the outer ones fixed; tongue and hyoid bone with similar depressible teeth; a single band of teeth on each side of palate. VOMER absent. BRANCHIOSTEGALS about 14. SCALES moderate; modified scales extending in a dorsal and a ventral series onto midcaudal rays. LATERAL LINE poorly marked. ANAL fin long, its origin about midway between head and base of caudal fin and closer to insertion of pelvic fin than to base of caudal fin; usually with only the last ray branched, and this to its base, but occasionally with the next to the last ray also branched; anal base much longer than dorsal base, its length 134.3–164.0 % of dorsal base length. DORSAL fin with some of anterior rays usually extending to tips of some succeeding rays when laid back; its origin generally closer to tip of snout than to adipose fin, but sometimes nearer adipose fin on some large specimens. PECTORAL fin with tip extending much beyond pelvic origin, and usually reaching dorsal origin. PELVIC fin with 8 rays, the median ones much longer than the outer rays; the 1st ray the shortest, usually the 6th, or occasionally the 7th, ray the longest. Pelvic bones with posterior processes long and narrow with a slight lateral flair in proximal fourth, slightly expanded laterally in proximal third with mid-dorsal ridge diminishing distally.

Species. The genus is monotypic with the single species widely distributed in the Atlantic, Indian, and western and central Pacific oceans.

Trachinocephalus myops (Forster) 1801

Lizardfish, Snakefish, Ground Spearing, Lagarto

Figures 8, 14, 15

Study Material. A total of 98 specimens ranging in length between 42 and 231 mm, from: Bermuda, and the United States Atlantic Coast, North Carolina to Florida Straits. One specimen, 137 mm, cove near Hunt's Bay, Bermuda, Sept. 21, 1905, CNHM 5463; 1, 42 mm, Long Bay, Cooper I., Bermuda, Sept. 25, 1905, CNHM 5464; 3, 43–84 mm, Murray's Anchorage, Bermuda, Aug. 2, 1948, CNHM 48306; 1, 129 mm, Combat St. 379, 34°59′N, 75°20′W, 35 fms., June 17, 1957, BLBG; 2, 125 and 219 mm, Combat St. 386, 34°45′N, 75°38′W, 45 fms., June 17, 1957, BLBG; 4, 110–175 mm, Combat St. 392, 34°36′N, 75°46′W, 30 fms., June 20, 1957, BLBG; 1, 65 mm, Pelican St. 188-2, 34°35′N, 76°05′W, 20 fms., March 1, 1940, USNM; 2, 185 and 205 mm, Combat St. 408, 34°23′N, 76°03′W, 30 fms., June 22, 1957, BLBG; 5, 105–165 mm, Combat St. 406, 34°17′N, 76°01′W, 45 fms., June 21, 1957, BLBG; 1, 143 mm, Pelican St. 187-2, 34°11′N, 76°18′W, 22 fms., Feb. 27, 1940, USNM; 1, 67 mm, Pelican St. 185-2, 34°03′N, 76°44′W, 20 fms., Feb. 16, 1940, USNM; 5, 118–170 mm, Combat St. 283, 32°56′N, 78°06′W, 50 fms., April 19, 1957, BLBG; 1, 122 mm, Pelican St. 194-10, 32°34′ N, 79°05′W, 19 fms., March 9, 1940, USNM; 1, 203 mm, Combat St. 424, 32°34′ N, 78°46′W, 24 fms., June 24, 1957, BLBG; 1, 125 mm, Combat St. 425, 32°32′ N, 79°55′W, 21 fms., June 24, 1957, BLBG; 1, 194 mm, Combat St. 427, 32°32′ N, 79°01′W, 35 fms., June 25, 1957, BLBG; 3, 112–148 mm, Combat St. 428, 32°17′ N, 79°10′W, 24–28 fms., June 25, 1957, BLBG; 2, 186 and 192 mm, Combat St. 515, 32°01′N, 79°36′W, 25–27 fms., Oct. 7, 1957, BLBG; 1, 68 mm, Pelican St. 181-6, 32°00′N, 80°20′W, 11 fms., Feb. 3, 1940, USNM; 1, 66 mm, Pelican St. 195-9, 31°46′N, 79°47′W, 24 fms., March 13, 1940, USNM; 1, 83 mm, Pelican St. 198-2, 30°58′N, 80°10′W, 22 fms., March 15, 1940, USNM; 1, 181 mm, Combat St. 353, 30°24′N, 80°20′W, 24 fms., June 3, 1957, BLBG; 1, 78 mm, Pelican St. 200-10, 30°21′N, 80°36′W, 19 fms., March 27, 1940, USNM; 3, 120–175 mm, Combat St. 496, 30°16′N, 80°21′W, 25 fms., Aug. 20, 1957, BLBG; 2, 175 and 190 mm, Combat St. 497, 30°13′N, 80°23′W, 25 fms., Aug. 20, 1957, BLBG; 1, 90 mm, Pelican St. 201-2, 29°59′N, 80°31′W, 23 fms., March 27, 1940, USNM; 3, 170–210 mm, Combat St. 339, 29°19′N, 80°18′W, 25 fms., June 1, 1957, BLBG; 1, 175 mm, Combat St. 341, 29°10′N, 80°20′W, 22 fms., June 1, 1957, BLBG; 1, 85 mm, Pelican St. 204-1, 29°06′N, 80°19′W, 18 fms., March 29, 1940, USNM; 1, 208 mm, Pelican St. 204-3, 28°59′N, 80°04′W, 50–100 fms., March 29, 1940, USNM; 1, 53 mm, Pelican (New) St. 67, 28°48′N, 79°53′W, 212 fms., June 13, 1956, BLBG; 1, 161 mm, Combat St. 320, 28°17′N, 80°08′W, 25 fms., April 28, 1957, BLBG; 1, 162 mm, Theodore N. Gill Cruise 2, St. Regular 4, 27°20′N, 80°04′W, April 23, 1953, BLBG.

Gulf of Mexico to Off South American Coast. One specimen, 215 mm, 25 mi. SW. of Panama City, Florida, April 19, 1958, BLBG; 1, 195 mm, *ca.* 35 mi. SE. of Pensacola, Florida, 30–35 fms., May 28, 1956, BLBG; 1, 205 mm, Silver Bay St. 93, 29°04′N, 85°16′W, 19–21 fms., July 26, 1957, BLBG; 5, 164–188 mm, Oregon St. 407, 21°38′N, 92°10′W, 29 fms., August 17, 1951, USNM; 7, 102–165 mm, Oregon St. 1048, 21°17′N, 91°18′W, 20 fms., May 13, 1954, USNM; 2, 132 and 146 mm, Oregon St. 1048, 21°17′N, 91°18′W, 20 fms., May 13, 1954, UF 5196; 7, 120–168 mm, Oregon St. 417, 20°45′N, 92°12′W, 27 fms., Aug. 18, 1951, USNM; 4, 162–167 mm, Oregon St. 428, 18°47′N, 92°00′W, 8 fms., Aug. 23, 1951, USNM; 2, 170 and 214 mm, Oregon St. 2262, 07°18′N, 56°49′W, 30–33 fms., Sept. 1, 1958, BLBG; 2, 110 and 130 mm, Oregon St. 2268, 06°53′N, 55°59′W, 23 fms., Sept. 2, 1958, BLBG; 1, 112 mm, Oregon St. 2035, 06°20′N, 52°51′W, 35 fms., Nov. 11, 1957, BLBG; 1, 131 mm, Oregon St. 2044, 05°52′N, 52°03′W, 40 fms., Nov. 12, 1957, BLBG; 5, 110–231 mm, Oregon St. 2063, 02°35′N, 48°14′W, 53 fms., Nov. 15, 1957, BLBG; 3, 80–170 mm, Oregon St. 2091, 00°33′N, 47°03′W, 20 fms., Nov. 18, 1957, BLBG.

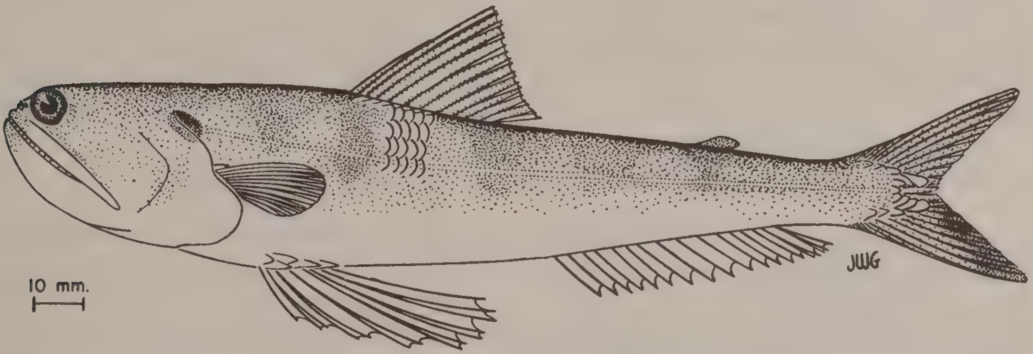

Figure 14. *Trachinocephalus myops*, 180 mm SL, Cape Lookout, North Carolina, Combat St. 392, 34°36′N, 75°46′W, 30 fms., BLBG.

Distinctive Characters. Those of the genus.

Description. Proportional dimensions in per cent of standard length, with ranges of proportions first, followed by the mean in parentheses, based on measurements from 13 specimens: 53, 67, 90, 110, 122, 140, 146, 167, 175, 185, 205, 219, and 231 mm SL.

Body at base of pelvic fin: depth 15.5–21.5 (18.7); width 12.9–17.4 (15.2).

Head: length 25.2–28.6 (27.1).

Snout: length 2.2–3.1 (2.7).

Eye: diameter 3.2–6.3 (4.4).

Interorbital: width 2.1–3.8 (2.8).

Premaxillary: length 12.3–17.0 (15.4).

Distance from snout to origin of: dorsal fin 38.1–41.6 (39.6); anal fin 62.0–66.2 (63.9); pelvic fin 29.1–34.4 (31.6).

Distance from: origin of dorsal fin to origin of adipose fin 40.2–43.3 (41.8); tip of pectoral fin to origin of pelvic fin +3.1 to +6.0 (+4.6).

Dorsal fin: length of base 14.1–20.0 (16.5); length of longest ray 17.0–22.3 (20.1); length of last ray 8.1–11.0 (9.8).

Anal fin: length of base 23.1–26.9 (24.2).

Pectoral fin: length of longest ray 10.4–12.4 (11.5).

Pelvic fin: length of first ray 6.8–9.0 (8.1); length of longest ray 23.4–28.4 (25.5).

Counts, based on 92 specimens.

Scales: predorsal 14–18 (2 specimens with 14, 6 with 15, 39 with 16, 30 with 17, 12 with 18); rows of complete scales between lateral line and base of dorsal fin 3 (all specimens).[3]

Lateral-line scales: 53–59 (3 with 53, 27 with 54, 27 with 55, 15 with 56, 17 with 57, 1 with 58, 1 with 59), 51–61 recorded (*6*: 57; *22*: 91).

Fin rays: dorsal fin 11–13 (4 with 11, 56 with 12, 31 with 13), 14 recorded (*6*: 57; *23*: 254; *50*: 20); anal fin 14–16 (26 with 14, 49 with 15, 16 with 16), 18 recorded (*20*: 199); pectoral fin 11–13 (6 with 11, 77 with 12, 9 with 13).

Vertebrae: 58 (*19*: 91).

Color. In preservative, adults (Fig. 14) mottled greyish brown on top and sides of head, and on back and sides of body to below the midline. About five rather indistinct broad saddles of darker brown on body, the 1st about midway between head and dorsal fin origin, the 2nd at dorsal origin, the 3rd at posterior end of dorsal base, the 4th midway between dorsal base and adipose fin, and the 5th at adipose fin. Belly pale with a yellowish cast. Opercle with a black spot at upper angle. Sides of body with narrow, greyish longitudinal stripes, usually about 4 in number (yellow in life), these prominent in small specimens but indistinct in larger specimens. Dorsal and caudal fins dusky; pectorals, pelvics, and anal fins pale (yellowish in life).

Size. The largest specimen we examined was 231 mm SL. Norman (*60*: 123) examined a stuffed specimen of 330 mm TL, and Fowler (*22*: 91) stated that the species reaches 375 mm—presumably a total length of about 15 inches. Poll (*66*: 76) reported a specimen of 225 mm TL as weighing 75 g.

Habits. Although this species is taken in inshore areas, our data for the western North Atlantic indicate that it is more abundant in an offshore bottom habitat. The extensive trawling activities of the U.S. Fish and Wildlife Service vessels PELICAN, OREGON, COMBAT, and SILVER BAY indicate a depth range to more than 200 fathoms, but with the great majority of records at 20 to 50 fathoms, on the mid-Continental Shelf area. The depth record for the species is 212 fathoms—a 53-mm SL specimen from off northeastern Florida.

Very little has been recorded of the behavior, breeding, food, or enemies. It has been recorded from sand, shell, rock, and mud bottoms. A habit of burrowing into a sand bottom, sometimes leaving the eyes exposed, has been described (*16*: 95; *50*: 20; *63*: 63). The young have been found washed ashore after rough weather (*61*: 251;

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[3] Fowler (*22*: 91) recorded the scales as "3 or 4 above to dorsal fin origin."

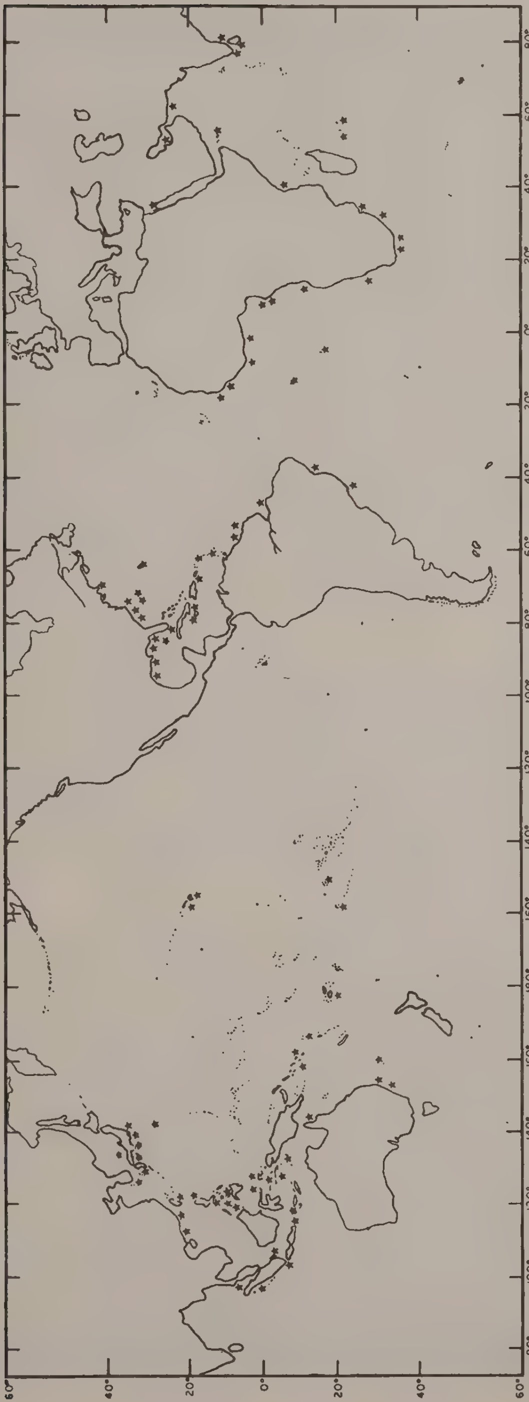

FIGURE 15. Distribution of *Trachinocephalus myops* (stars).

74: 148). A foot-long male with nearly ripe milt was recorded from St. Helena about March (*16*: 95); a 168-mm female in full breeding condition was taken in July at the Grenadines, B.W.I. (*5*: 211–212); and six males in advanced maturation were taken off West Africa (*66*: 75). This species has been identified from the stomach contents of *Eulamia milberti* (Müller and Henle) and *E. obscura* (LeSueur) (*73*: 175) and of *Thunnus atlanticus* (Lesson) (*5*: 212). A 168-mm TL specimen was reported to have contained a 106-mm TL *Xyrichthys infirmus* Bean (*5*: 212).

Relation to Man. The species has no significant relation to man. Larger specimens are sometimes caught during bottom fishing.

Range. Fig. 15. This species is almost circumtropical in distribution, having been reported from continental and insular waters from the Gulf of Mexico eastward to the islands of Polynesia. It has not been recorded, however, from the eastern Pacific off the American continents. In the western North Atlantic the species infrequently occurs as far north as Cape Cod. It is more common off the coast of North Carolina southward and is taken to Brazil. Within this broad area it has been taken at Bermuda, off the coast of the United States from Cape Cod to Florida, in the Bahamas, Cuba, numerous localities in the West Indies, Jamaica, Gulf of Mexico, and off Brazil to about the equator.

Synonyms and References:

Salmo foetens (*non* Linnaeus) Bloch, Naturg. ausländ. Fische, *8*, 1794: 118, pl. 384, fig. 2 (descr., off Carolina); Bloch and Schneider, Syst. Ichthyol., 1801: 404 (descr. after Bloch 1794); Cuvier, Règne Anim., *1*, 1817: 169 (ref. after Bloch 1794); Cuvier, Règne Anim., ed. 2, *2*, 1829: 314 (copied from Cuvier 1817); Griffith, Anim. Kingd., 1834: 430 (transl. Cuvier 1829); Valenciennes, Poissons *in* Règne Anim., ed. 3, *2*, 1837: 268 (copied from Cuvier 1829); Swainson, Nat. Hist. Fish. Amphib. Rept., 1838: 246 (ref. *fide* Norman 1935: 122); Temminck and Schlegel, Pisces, Fauna Japon., *5*, 1846: 231 (ref. to Bloch 1794); Valenciennes *in* Cuvier and Valenciennes, Hist. Nat. Poiss., *22*, 1849: 489 (ref. after Bloch 1794).

Salmo myops Forster *in* Bloch and Schneider, Syst. Ichthyol., 1801: 421 (descr. from Forster's ms; type loc., St. Helena; no type spec. designated); Cuvier, Règne Anim., ed. 2, *2*, 1829: 314 (ref.); Griffith, Anim. Kingd., 1834: 430 (ref. transl. Cuvier 1829); Valenciennes, Poissons *in* Règne Anim., ed. 3, *2*, 1837: 268 (ref. copied from Cuvier 1829); Lichtenstein, Descr. Anim. Observ. I. R. Forster, 1844: 412 (Forster's ms. descr.; St. Helena); Valenciennes *in* Cuvier and Valenciennes, Hist. Nat. Poiss., *22*, 1849: 488 (ref. St. Helena).

Osmerus lemniscatus Lacépède, Hist. Nat. Poiss., *5*, 1803: 230 (descr.), 236 (based on Plumier, pl. 6, fig. 1; type loc. Martinique; no type spec. designated); Temminck and Schlegel, Pisces, Fauna Japon., *5*, 1846: 231 (ref. to Lacépède); Valenciennes *in* Cuvier and Valenciennes, Hist. Nat. Poiss., *22*, 1849: 488 (ref.).

Saurus truncatus Spix, Selecta Gen. Sp. Piscium, 1829: 82, pl. 45 (type loc. Brazil; descr. from 6- and 7-inch specimens, in Museo Monacensi); 1831: pl. D (scales ill.); Cuvier, Règne Anim., ed. 2, *2*, 1829: 314 (ref.); Griffith, Anim. Kingd., 1834: 430 (ref.); Valenciennes, Poissons *in* Règne Anim., ed. 3, *2*, 1837: 268 (ref.); Valenciennes *in* Cuvier and Valenciennes, Hist. Nat. Poiss., *22*, 1849: 489 (ref. to Spix); Castelnau, Exped. Cent. Amer. Sud, Poissons, *3*, 1855 (consid. synon. *S. lemniscatus* Lacépède; Rio de Janeiro); Poey, Memorias, *2* (2), 1860: 305 (*cf. S. brevirostris* Poey).

Saurus limbatus Eydoux and Souleyet, Voy. aut. du Monde La Bonité, *1* (2), 1841: 199, pl. 7, fig. 3 (no type loc. or type spec. designated).

Saurus trachinus Temminck and Schlegel, Pisces, Fauna Japon., *5*, 1846: 231, pl. 106, fig. 2 (type loc., Japan; holotype LMNH 3228, designated by Boeseman, Zoöl. Meded., 28, 1947: 171, paratypes LMNH 1814, 1929, 3227a, 3227b); Cantor, J. Roy. Asiatic Soc. Beng., *18* (2), 1849–1850: 1253 (descr.; Penang; Japan); Bleeker, Verh. Batavia Genoot., *24*, 1852: 29 (descr.; Amboina, Moluccas); Bleeker, Naturrk. Tijdschr. Ned.-Ind., *3*, 1852: 235, 250, 291 (descr.; Amboina, Wahai, and Bangka, Moluccas); Bleeker, Naturrk. Tijdschr. Ned.-Ind., *3*, 1852: 446 (Bangka I., Indonesia); Jouan, Mem. Soc. imp. Sci. Nat. Cherbourg, *13*, 1867: 271 (Hong-Kong; excluding from synon. *Saurus elegans* Gray and *S. fasciolatus* Less.); Jouan, Mem. Soc. imp. Sci. Nat. Cherbourg, *13*, 1868: 271 (Hong-Kong; *fide* Fowler, Hong-Kong Nat., *3* [3–4], 1932: 256); Boeseman, Zoöl. Meded., *28*, 1947: 171 (Temminck and Schlegel's 1846 spec. descr.; holotype designated).

Saurus lemniscatus, Richardson, Rep. Ichthyol. Seas of China and Japan, 1846: 301 (China Sea).

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Trachinocephalus trachinus, Jordan and Snyder, Proc. U.S. nat. Mus., *23* (1213), 1900: 350 (Tokyo, Japan); Jordan and Evermann, Proc. U.S. nat. Mus., *25* (1289), 1902: 329 (Keerun, Formosa).

Synodus (*Trachinocephalus*) *myops*, Steindachner, Denkschr. Akad. Wiss. Wien, *71* (1), 1907: 154 (Ras Shoab; Gischin; Socotra I., Indian O.).

Saurus (*Trachinocephalus*) *myops*, Metzelaar, Rapp. Bet. Voor. Ind. Zee. Kol. Curaçao, *2* (2), 1919: 23 (St. Eustatius, Leeward Is.); Delsman, Treubia, *16*, 1938: 418 (larvae; Java Sea).

Trachinocephalus hypozona, Whitley, Fish. Bull. W. Aust. Fish. Dept., *2*, 1948: 13 (Australia).

Questionable References:

Trachinocephalus myops, Rosen, Lunds Univ. Årsskr., *2* (7), 1911: 49 (Nassau and Clarence Harbor, Bahamas; no descr. or corroborating specimens).

Trachinocephalus myops, Anderson and Gehringer, U.S. Fish Wildl. Serv., Sp. Sci. Rep. Fish. 234, 1957: 56 (larval spec.; 24°28′N, 77°28′W, Tongue of the Ocean, Bahamas).

Negative References:

Not *Trachinocephalus myops* (Forster), Bean, Fish. Bahama Is., 1905: 297 (ref. is to spec. of *Synodus saurus* from Bahama Is.); Regan, Rep. Brit. Antarc. Exped., 1910, *1* (1), 1914: 22 (22°56′S, 41°34′W, off Cape Frio, Brazil; the 80-mm spec. designated holotype of *Saurida brasiliensis* by Norman, Proc. zool. Soc. London, 1935: 125); Hildebrand, Smithsonian misc. Coll., *110* (9), 1948: 12 (designated as types of *Synodus cinereus*; ref. is to *S. saurus*).

Genus *Synodus* Gronow 1763

Lizardfishes

Synodus Gronow, Zoophyl., 1763: 112; type species by absolute tautonymy, *Esox synodus* Linnaeus 1758, after Gronow, Mus. Ichthyol., *2*, 1756: 4, pl. 7, fig. 1.

Generic Synonyms:[4]

Soarus Linck, Mag. Physik Naturg., Gotha, *6* (3), 1790: 37; type species *Salmo saurus* Linnaeus 1758; *Soarus* evidently altered orthography for *Saurus*, *fide* Fowler 1936: 341.

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[4] Whitley (*76*: 219), using Norman's 1935 key characters for definition, proposed seven genera for *Synodus* Gronow. Five of these were new; he recognized *Synodus* Gronow (type species, *Esox synodus* Linnaeus) and *Tirus* Rafinesque (type species, *Salmo saurus* Linnaeus; with generic synonyms *Saurus* Cuvier, *Alpismaris* Risso, and *Laurida* Swainson). He further proposed a new subgenus, *Newtonscottia* (type species, *Synodus houlti* McCulloch), of *Synodus* Gronow.

Tirus Rafinesque, Carett. n. gen., 1810: 56; type species by monotypy, *Tirus marmoratus* Rafinesque 1810.

Saurus Cuvier, Règne Anim., *1*, 1817: 169; type species by absolute tautonymy, *Salmo saurus* Linnaeus 1758.

Alpismaris Risso, Hist. Nat. Europe Merid., *3*, 1826: 458; type species *Stolephorus risso* Risso 1810, by subsequent designation of Jordan, 1917: 120, *fide* Fowler, 1936: 341.

Laurida Swainson, Nat. Hist. Fish. Amphib. Rept., 1, 1838: 242; type species by original designation, *Laurida mediterranea* Swainson 1838; Swainson, Nat. Hist. Fish. Amphib. Rept., *2*, 1839: 288.

Negotirus Whitley, Aust. Zool., *8* (4), 1937: 219; type species by original designation, *Synodus evermanni* Jordan and Bollman 1890.

Austrotirus Whitley, Aust. Zool., *8* (4), 1937: 219; type species by original designation, *Synodus similis* McCulloch 1921.

Allouarnia Whitley, Aust. Zool., *8* (4), 1937: 219, type species by original designation, *Synodus sageneus* Waite 1905.

Exotirichthys Whitley, Aust. Zool., *8* (4), 1937: 219; type species by original designation, *Saurus altipinnis* Günther 1864.

Esosynodus Whitley, Aust. Zool., *8* (4), 1937: 219; type species by original designation, *Saurus lucioceps* Ayres 1855.

Characters. BODY slender and cylindrical, the depth and width at origins of pelvic fins about equal. HEAD depressed or but slightly depressed; bone surfaces on top of head more or less rugose. EYE with a narrow adipose eyelid on anterior and posterior margins. INTERORBITAL space moderately concave. SNOUT triangular, more nearly pointed than blunt, shorter or longer than eye diameter. LOWER JAW included or extending beyond upper jaw, a fleshy knob at tip present or absent. TEETH in the upper jaw large, compressed, and pointed, in a narrow band, with the inner ones larger and depressible; a band of similar teeth in lower jaw, with the inner ones larger and depressible, and the outer ones fixed; tongue and hyoid bone with similar depressible teeth; a single band of teeth on each side of palate. VOMER absent. BRANCHIOSTEGALS 12–18. SCALES small to large; modified scales extending in a dorsal and a ventral series onto midcaudal rays. LATERAL LINE well marked or only slightly pronounced, with or without a slight keel on caudal peduncle formed by pored scales. ANAL fin short, its origin much nearer to base of caudal than to head; the first 2 rays always unbranched, frequently others unbranched, but the last ray always branched to its base; anal base much shorter, or longer, than dorsal base. DORSAL fin with anterior rays falling short of, or reaching beyond, the tips of succeeding rays when laid back; its origin varying from nearer to snout to nearer to adipose fin. PECTORAL with tip falling short of, or extending past, pelvic origin, and usually not reaching, but occasionally extending to, dorsal origin. PELVIC fin with 8 rays, the median ones much longer than the outer rays; the 1st ray the shortest, usually the 6th or 7th ray the longest. Pelvic bones with posterior processes long and narrow, or long, flat, and broad with acute tip and with a mid-dorsal ridge.

Species. A survey of the literature on the genus *Synodus* indicates that 23 species [excluding *Xystodus sageneus* (Waite), which may be determined to belong here] may be recognized from various parts of the world. Of these 18 occur in Indo-Pacific waters[5] but apparently not in the Mediterranean Sea or Atlantic Ocean; the interspecific relationships of some of these species are uncertain. The five species that occur in the Atlantic Ocean have never been reliably reported from the Indo-Pacific; two of these occur in the Mediterranean and eastern Atlantic, and all five species have been represented in study material from the western North Atlantic.

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[5] *Synodus variegatus* (Lacépède) 1803, *S. lucioceps* (Ayres) 1855, *S. altipinnis* (Günther) 1864, *S. indicus* (Day) 1873, *S. kaianus* (Günther) 1880, *S. scituliceps* Jordan and Gilbert 1882, *S. evermanni* Jordan and Bollman 1890, *S. lacertinus* Gilbert 1890, *S. simulans* Garman 1899, *S. fuscus* Tanaka 1917, *S. hoshinonis* Tanaka 1917, *S. macrops* Tanaka 1917, *S. houlti* McCulloch 1921, *S. sechurae* Hildebrand 1946, *S. marchenae* Hildebrand 1946, *S. binotatus* Schultz 1953, *S. englemani* Schultz 1953, *S. ulae* Schultz 1953.

Key to Atlantic Species

1a. Scales in lateral line 43–50 (rarely 51 or 52).
  2a. Dorsal fin with anterior rays not extending beyond, but occasionally extending to, tips of some of the succeeding rays when laid back; lower jaw rounded anteriorly, without fleshy knob; a black patch on shoulder girdle under gill cover. *intermedius* (Spix) 1829, below.
  2b. Dorsal fin with anterior rays extending to, and usually beyond, tips of succeeding rays when laid back; lower jaw ending in a fleshy knob; no black patch on shoulder girdle under gill cover. *poeyi* Jordan 1887, p. 54.
1b. Scales in lateral line 55–64 (rarely 54 or 65).
  3a. Three rows of complete scales between lateral line and base of dorsal fin. *saurus* (Linnaeus) 1758, p. 59.
  3b. Four to six rows of complete scales between lateral line and base of dorsal fin.
    4a. Anal rays 11–13 (rarely 10 or 14); anal base 82.5–125 % of dorsal base, thus about equal to, or usually longer than, dorsal base (rarely shorter); tip of pectoral fin falling short of, or reaching base of, pelvic fin; predorsal scales 20–30 (usually in an irregular row; difficult to count). *foetens* (Linnaeus) 1766, p. 65.
    4b. Anal rays 8–10 (rarely 11); anal base 53–65.8 % of dorsal base, thus much shorter than dorsal base; tip of pectoral fin extending much beyond base of pelvic fin; predorsal scales 15–18. *synodus* (Linnaeus) 1758, p. 78.

Synodus intermedius (Spix) 1829

Lizardfish, Sand diver, Galiwasp

Figures 16–18

Study Material. A total of 41 specimens ranging in length between 52 and 260 mm, from: ATLANTIC COAST OF THE UNITED STATES, NORTH CAROLINA TO FLORIDA. One specimen, 172 mm, PELICAN St. 185-2, 34°03′N, 76°44′W, 20 fms., Feb. 16, 1940, USNM; 2, 200 and 210 mm, COMBAT St. 283, 32°56′N, 78°06′W, 50 fms., April 19, 1957, BLBG; 1, 212 mm, COMBAT St. 519, 31°49′N, 79°31′W, 45 fms., Oct. 8, 1957, BLBG; 1, 200 mm, COMBAT St. 526, 31°38′N, 79°40′W, 41–45 fms., Oct. 8, 1957, BLBG; 1, 213 mm, PELICAN St. 179-4, 31°28′N, 79°46′W, 25 fms., Feb. 1, 1940, USNM; 1, 69 mm, Pelican St. 197-7, 31°09′N, 80°09′W, 23 fms., March 15, 1940, USNM; 1, 205 mm, Combat St. 497, 30°13′N, 80°23′W, 25 fms., Aug. 20, 1957, BLBG; 1, 230 mm, Combat St. 323, 29°52′N, 80°13′W, 175 fms., May 30, 1957, BLBG; 1, 198 mm, Combat St. 333, 28°58′N, 80°13′W, 30 fms., June 1, 1957, BLBG.

Gulf of Mexico, and Caribbean Sea to Brazil. One specimen, 233 mm, near Destin, Florida, June 1958, BLBG; 2, 240 and 260 mm, Silver Bay St. 314, 30° 00′N, 86°37′W, 30 fms., March 16, 1958, BLBG; 1, 219 mm, Pelican St. 157-1, 29°28′N, 84°48′W, 11 fms., March 11, 1939, USNM; 1, 117 mm, Oregon St. 1719, 29°00′N, 83°32′W, 8 fms., Feb. 16, 1957, BLBG; 1, 52 mm, Silver Bay St. 53, 28°33′N, 84°24′W, 20 fms., July 16, 1957, BLBG; 1, 167 mm, Oregon St. 1020, 24°47′N, 83°18′W, 35 fms., April 19, 1954, USNM; 2, 135 and 195 mm, Silver Bay St. 438, 23°36′N, 87°54′W, 68 fms., May 18, 1958, BLBG; 1, 190 mm, Silver Bay St. 431, 23°13′N, 89°00′W, 57 fms., May 17, 1958, BLBG; 1, 180 mm, Silver Bay St. 398, 22°29′N, 90°03′W, 37 fms., May 11, 1958, BLBG; 1, 215 mm, Silver Bay St. 411, 22°11′N, 88°53′W, 23 fms., May 14, 1958, BLBG; 2, 138 and 208 mm, Oregon St. 407, 21°38′N, 92°10′W, 29 fms., Aug. 17, 1951, USNM; 3, 197–245 mm, Pedro Bay, St. Elizabeth, Jamaica, 20 fms., Oct. 11, 1950, IJ; 1, 90 mm, Oregon St. 1873, 16°40′N, 82°12′W, 56 fms., Aug. 22, 1957, BLBG; 1, 94 mm, Oregon St. 1865, 16°20′N, 83°20′W, 42 fms., Aug. 21, 1957, BLBG; 2, 72 and 79 mm, Oregon St. 1937, 16°02′N, 82°07′W, 21 fms., Sept. 15, 1957, BLBG; 4, 169–215 mm, Oregon St. 1934, 16°00′N, 82°05′W, 21 fms., Sept. 15, 1957, BLBG; 1, 191 mm, Oregon St. 1935, 15°57′N, 82°06′W, 21 fms., Sept. 15, 1957, BLBG; 4, 142–205 mm, Oregon St. 2262, 07°18′N, 56°49′W, 30–33 fms., Sept. 1, 1958, BLBG; 1, 152 mm, Oregon St. 2265, 06°56′N, 56°43′W, 21 fms., Sept. 2, 1958, BLBG.

Distinctive Characters. See *Key to Atlantic Species*, p. 48.

Description. Proportional dimensions in per cent of standard length, with ranges given first, followed by the mean in parentheses, based on measurements from 14 specimens: 52, 69, 79, 90, 117, 138, 167, 169, 191, 205, 208, 213, 219, and 260 mm SL.

Body at base of pelvic fin: depth 10.2–16.2 (13.3); width 10.6–16.1 (14.0).

Head: length 23.4–29.6 (25.8).

Snout: length 3.1–7.9 (5.4).

Eye: diameter 4.4–7.7 (5.6).

Interorbital: width 2.7–6.7 (4.2).

Premaxillary: length 12.2–18.8 (15.3).

Distance from snout to origin of: dorsal fin 37.9–42.5 (40.5); anal fin 69.0–74.6 (71.4); pelvic fin 31.7–37.9 (34.4).

Distance from: origin of dorsal fin to origin of adipose fin 37.0–42.2 (39.5); tip of pectoral fin to origin of pelvic fin + 1.4 to + 5.1 (+ 3.3).

Dorsal fin: length of base 14.8–18.5 (16.4); length of longest ray 15.1–18.7 (16.6); length of last ray 6.2–8.8 (7.9).

Anal fin: length of base 12.4–16.6 (14.1).

Pectoral fin: length of longest ray 11.3–13.7 (12.4).

Pelvic fin: length of first ray 9.0–11.9 (10.2); length of longest ray 15.2–23.4 (20.5).

Counts, based on 38 specimens.

Scales: predorsal 14–17 (9 specimens with 14, 17 with 15, 7 with 16, 4 with 17); rows of complete scales between lateral line and base of dorsal fin 3 (all specimens)[6].

Lateral-line scales: 45–52 (1 with 45, 3 with 46, 8 with 47, 15 with 48, 5 with 49, 4 with 50, 0 with 51, 1 with 52).

Fin rays: dorsal fin 11–13 (6 with 11, 28 with 12, 4 with 13); anal fin 10–12 (2 with 10, 27 with 11, 9 with 12); pectoral fin 11–13 (5 with 11, 24 with 12, 8 with 13).

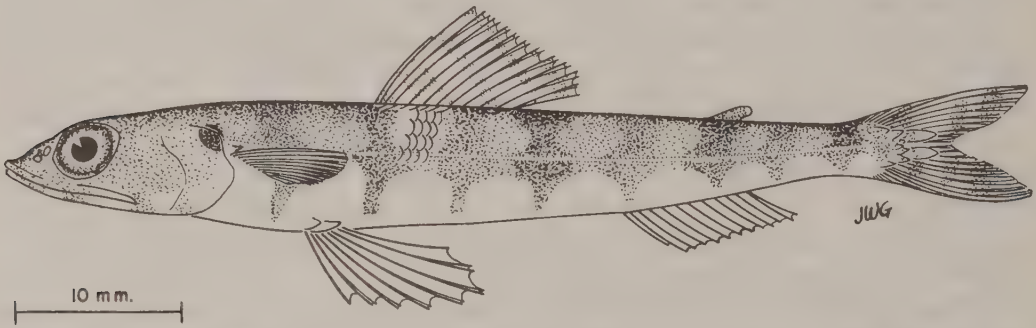

FIGURE 16. *Synodus intermedius*, 52.0 mm SL, off Apalachicola, Florida, SILVER BAY St. 53, 28°33′N, 84°24′W, 20 fms., BLBG.

HEAD depressed; top of head only slightly rugose. SCALES large. LATERAL LINE well marked, with a slight keel on caudal peduncle. SNOUT short and blunt, shorter to longer than eye diameter. INTERORBITAL space markedly concave. LOWER JAW included in, or subequal to, upper jaw, rounded at tip and not ending in a fleshy knob. DORSAL fin with anterior rays extending not beyond, but occasionally to, tips of succeeding rays when laid back; its origin about equidistant between adipose fin and tip of snout. ANAL base shorter than dorsal base (rarely equal to dorsal base), its length 78.7–100.0 % of dorsal base length. PECTORAL fin with tip extending beyond origin of pelvic fin. PELVIC fin with 6th or 7th ray the longest. PELVIC BONES with posterior processes long, flat, and broad with acute tip and a mid-dorsal ridge diminishing distally.

Color. In preservative, adults (Fig. 17) usually brownish grey on head, back, and upper sides, with about eight cross-bands, widest at the lateral line and extending downward well onto the sides. Usually smaller patches of color between these bars. Belly light. Pectoral fins dusky; dorsal fin with a barred pattern; caudal dusky, with lower lobe darker than remainder of fin; pelvic and anal fins pale; adipose fin dark. A black oval spot on shoulder girdle partly concealed by upper edge of gill cover. Basic adult color pattern similar in young (Fig. 16), but crossbands much more distinct.

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[6] The following counts of rows of scales above the lateral line do not agree with ours; Fowler (*21*: 342) gave a count of 4 scales; Evermann and Marsh (*19*: 92) gave a count of 5 scales.

Size. The largest specimen examined was 260 mm SL. Norman (*60*: 105) recorded a specimen of 380 mm TL, and Jordan (*40*: 108) recorded one of 18 inches, both from Key West, Florida.

Habits. As with *S. poeyi*, its closest relative, this is apparently a species of offshore bottoms that seldom inhabits the shore areas. The extensive trawling activities of the PELICAN, OREGON, COMBAT, and SILVER BAY indicated a depth distribution of 8 to 175 fathoms, with the vast majority of the records between 20 and 60 fathoms. The depth record for the species is 175 fathoms—a 230-mm SL specimen from off northeastern Florida.

Little is known of the habits of *S. intermedius*, but an unsubstantiated statement has been made that its habits are similar to those of *S. foetens* (*11*: 77). The species was said to be common about rocks at Key West (*40*: 108) and large specimens were sometimes found in shallow water at Tortugas, Florida (*50*: 21).

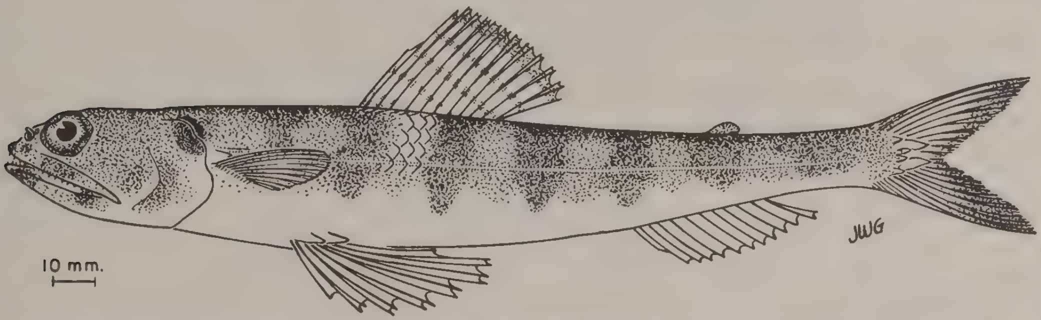

FIGURE 17. *Synodus intermedius*, 205 mm SL, off Jacksonville, Florida, COMBAT St. 497, 30°13′N, 80°23′W, 25 fms., BLBG.

This has been reported as a carnivorous species, feeding on fish, especially engraulids and atherinids, and on shrimp (*7*: 60).

One predator has been reported, for the species has been found in the stomachs of red snappers, *Lutjanus blackfordi* Goode and Bean, from the snapper banks off Pensacola, Florida (*43*: 143). Digenetic trematodes have been reported as parasites (*51*: 375).

Relation to Man. Not occurring regularly inshore, taken incidental to other fishing operations in but few areas, and then not utilized, the species has little direct value to man. It was reported as one of the poorer foodfish brought into the markets of Haiti (*7*: 60). Specimens have been taken rarely by sport fishermen (*5*: 21).

Relationship to Extralimital Species. Based on key characters and descriptions given by Norman (*60*) and Matsubara (*53*), the range of lateral-line scales of *S. intermedius* (45–52) overlaps that of *S. fuscus* Tanaka and *S. macrops* Tanaka, each with a range of 49–55, and of *S. hoshinonis* Tanaka with a range of 52–54. *S. intermedius* is distinguished from *S. fuscus* by the absence of the opercular spot present on *S. fuscus*. *S. intermedius* has a longer anal base than *S. macrops* and *S. hoshinonis* (12.4–16.6% of SL in *S. inter-*

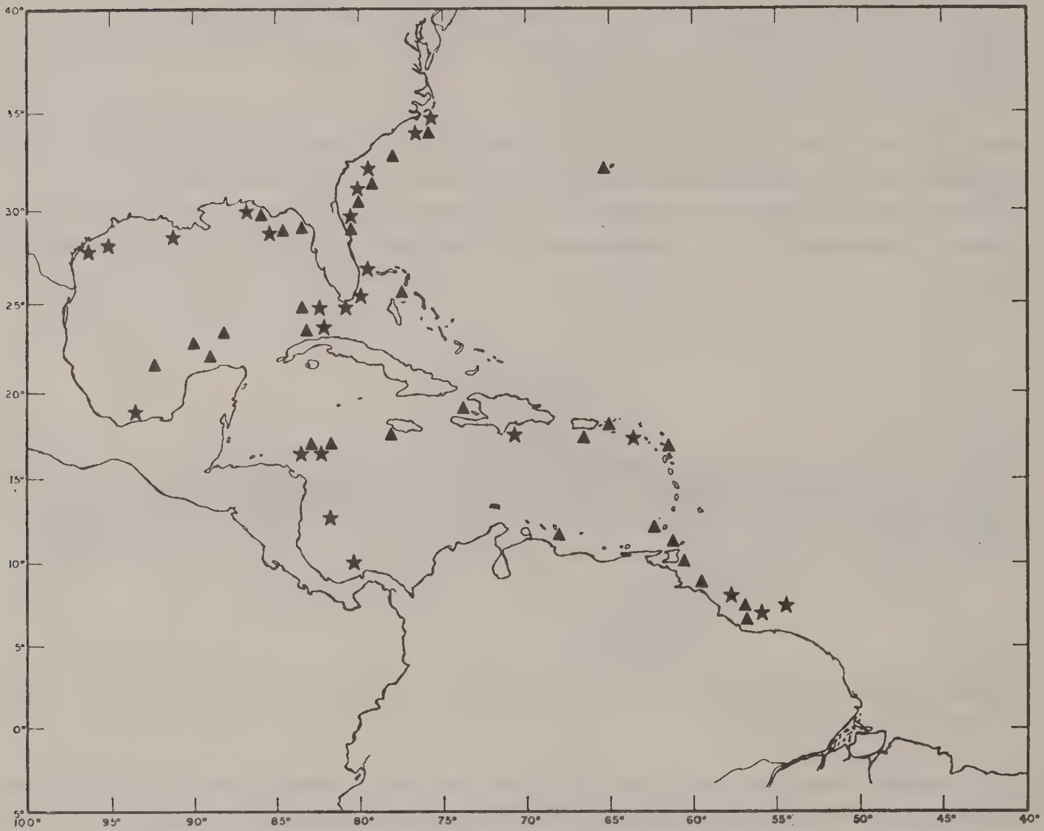

FIGURE 18. Distribution of *Synodus intermedius* (triangles) and *Synodus poeyi* (stars).

medius, 9.1–9.8 % in *S. hoshinonis*, 9.1–11.1 % in *S. macrops*); and *S. intermedius* has a broad posterior pelvic process, contrasted with the slender process of *S. macrops*. *S. intermedius* differs from *S. marchenae* in having more anal rays (8–9 in the latter).

Range. Fig. 18. This species ranges on the Atlantic coast of America from North Carolina to Brazil. Within this area it has been reported from Bermuda, the coast of the United States from North Carolina to southern Florida, the northern and southern Gulf of Mexico, Cuba, Jamaica, eastern Caribbean Sea, West Indies, and Brazil. One unsubstantiated record of the species from off French Equatorial Africa is doubtful (*64*: 179).

Synonyms and References:

Saurus intermedius Spix, Selecta Gen. Spec. Piscium, 1829: 81, pl. 44 (type loc., Brazil; type spec. loc. unknown, descr. from spec. 8.5 inches long, in Museo Monacensi), 1831: pl. D (scales ill.); Cuvier, Règne Anim., ed. 2, *2*, 1829: 314 (ref.); Griffith, Animal Kingd., 1834: 430 (ref.); Valenciennes, Poissons *in* Règne Anim., ed. 3, *2*, 1837: 268 (ref.); Castelnau, Exped. Cent. Amer. Sud, Poiss., *3*, 1855 (Bahia, Brazil); Günther, Cat. Fish. British Mus., *5*, 1864: 396 (descr.; Jamaica; Demerara, Brit. Guiana; Bahia, Brazil); Poey, Repert. Fisico-Nat. Cuba, *1* (13–14), 1866: 382 (discuss.); Poey, Repert. Fisico-Nat. Cuba, *2*

(13–20). 1868: 414 (Cuba? as *sp. dubia*); Günther, Rep. Shore Fish. Voy. 'Challenger,' *1* (6), 1880: 9 (Bermuda); Meek, Proc. Acad. nat. Sci. Philad., 1884: 133 (name by ref.; "According to Poey, the species figured by Spix lacks the scapular spot."); Günther, Rep. Deep-Sea Fish. Voy. 'Challenger,' *22*, 1887: 179 ("Probably descends to moderate depths."); Jordan, Proc. U.S. nat. Mus., *9* (593), 1887: 526 (*intermedius* Poey not *intermedius* Spix); Jordan, Rep. U.S. Comm. Fish and Fish. (1885), *13* (24), 1887: 827 (same as Jordan 1887: 526); Weber and de Beaufort, Fishes Indo-Austral. Archipel., *2*, 1913: 146 (part; descr.; W. Indies spec.; excl. Günther 1864: 396 from synon. and distr. rec. from Arafura Sea).

Saurus anolis Valenciennes *in* Cuvier and Valenciennes, Hist. Nat. Poiss., *22*, 1849: 483 (type loc., Martinique and Guadaloupe, Lesser Antilles, and Bahia, Brazil; type spec., MNHN A8611 and B1022, 390 and 400 mm respect., from Martinique; *fide* Bertin and Estève Impremerie Nat., 6, 1950: 7); Poey, Repert. Fisico-Nat. Cuba, *1* (13–14), 1866: 382 (ref.); Poey, Repert. Fisico-Nat. Cuba, *2* (13–20), 1868: 414 (ref.); Poey, An. Soc. esp. Hist. Nat., *5* (1), 1876: 143 (ref.); Meek, Proc. Acad. nat. Sci. Philad., 1884: 134 (report on type from Bahia in Mus. Paris, 245 mm long, 54 lateral-line scales, black spot on scapular part of gill openings); Bertin and Estève, Impremerie Nat., 6, 1950: 6 (syntypes reported in Paris Mus.).

Synodus cubanus Poey, An. Soc. esp. Hist. Nat., *5* (1), 1876: 143 (descr. from a 375-mm spec.; type loc. Cuba; type spec. deposition not known); Jordan, Proc. U.S. nat. Mus., *7* (416), 1884: 108 (descr.; Key West and Pensacola, Florida); Jordan, Bull. U.S. Fish. Comm., *4*, 1884: 79 (Key West, Florida); Jordan, Rep. U.S. Comm. Fish and Fish. (1885), *13* (24), 1887: 827 (by ref. to Poey, Enum. Pisc. cubens., 1876: 143).

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Agricola. São Paulo, 1940: 191 (Pernambuco, Brazil; *fide* Carvalho, Bol. Inst. Paul. Oceanogr., *2* (1), 1950: 107); Longley and Hildebrand, Publ. Carnegie Instn. Wash., *34* (535), 1941: 21 (descr., color, shallow water to 60 fms.; *cf. S. poeyi*; Tortugas, Florida); Fowler, Arqu. Zool. estad. São Paulo, *3* (6), 1941: 140 (Bahia, Brazil); Hildebrand, Copeia, 1941: 224 (off Beaufort Inlet and in Gulf Stream off Beaufort, N. Carolina); Fowler, Fish Culturist, *21* (9), 1942: 66 (in Museo Poey and Colegio de la Salle, Cuba); Herre, Stanford Univ. Publ., Univ. Ser., Biol. Sci., *7* (2), 1942: 290 (English Harbor, Antigua, B.W.I.); Fowler, Monogr. Acad. nat. Sci. Philad., *6*, 1944: 438 (Bahamas); Manter, Amer. Midl. Nat., *38* (2), 1947: 345, 358, 375 (digenetic trematodes; Tortugas, Florida); Hildebrand, Smithson. misc. Coll., *110* (9), 1948: 12 (*cf. S. cinereus*); Breder, Field Bk. Mar. Fish. Atlantic Coast, new ed., 1948: 77 (genl.); Carvalho, Bol. Inst. Paul. Oceanogr., *2* (1), 1950: 107 (after Ihring 1940: 191; Pernambuco, Brazil); Buller, U.S. Fish Wildl. Serv., Sp. Sci. Rep. Fish. 58, 1951: 12 (s. Atl. coast U.S.); Fowler, Mem. Soc. cubana Hist. nat., *21* (1), 1952: 86 (descr.; Port-au-Prince area, Haiti); Hildebrand, Publ. Inst. mar. Sci. Texas, *4* (1), 1955: 201 (w. of Campeche, México), 222 (listed); Springer and Bullis, U.S. Fish Wildl. Serv., Sp. Sci. Rep. Fish. 196, 1956: 54 (OREGON St., Gulf of Mexico; record confirmed for St. 407); Robins, Fla. Bd. Conserv., Ed. Ser., *12*, 1958: 14 (Florida); Briggs, Bull. Fla. St. Mus., Biol. Sci., *2* (8), 1958: 257 (range); Gibbs, Copeia 1959: 233 (ref.).

Synodus anolis, Meek, Proc. Acad. nat. Sci. Philad., 1884: 133 (key; synonymy in part; Key West, Florida); Jordan, Proc. U.S. nat. Mus., *9* (593), 1887: 526 (ref.); Jordan, Proc. U.S. nat. Mus., *9* (593), 1887: 563 (listed); Jordan, Rep. U.S. Comm. Fish and Fish. (1885), *13* (24), 1887: 827 (listed; ref.).

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Questionable References:

Saurus intermedius, Osorio, J. Sci. math. phys. nat. acad. Real Sci. Lisboa, (2) *3* (11), 1894: 179 (St. Thomas I., Gulf of Guinea, W. Africa; no descr., no corraborating spec.); Osorio, J. Sci. math. phys. nat. acad. Real Sci. Lisboa, (2) *5* (19), 1898: 199 (St. Thomas I., W. Africa); Metzelaar, Rapp. Bet. Voor. Ind. Zee. Kol. Curaçao, *2* (2), 1919: 214 (based on Osorio 1894; St. Tomé, W. Africa).

Negative References:

Not *Saurus intermedius* Spix, Günther, Rep. Shore Fish. Voy. 'Challenger,' *1* (6), 1880: 50 (ref. is to *Synodus similis* McCulloch, spec. in British Mus. [Nat. Hist.] ident. by Norman 1935: 115; Arafura Sea); Delsman, Treubia, *16*, 1938: 418 (ref. is to an Indo-Pacific species); Whitley, Aust. Zool., *10* (2), 1943: 174 (stated: records of this species from Arafura Sea may refer to *Xystodus sageneus* Waite).

Not *Synodus intermedius* (Spix), Meek, Proc. Acad. nat. Sci. Philad., 1884: 132 (descr. spec. named *Synodus poeyi* by Jordan Proc. U.S. nat. Mus., 9 (593), 1887: 526; Havana, Cuba); Herre, Philippine Exped. Fish. Hong Kong, *8*, 1934: 23 (ref. it to *Synodus similis* from Culion, Philippines; *fide* Herre, U.S. Fish Wildl. Serv., Res. Rept. 20, 1953: 140).

Synodus poeyi Jordan 1887

Lizardfish

Figures 18–20

Study Material. A total of 137 specimens ranging in length between 36 and 200 mm, from: ATLANTIC COAST OF THE UNITED STATES, NORTH CAROLINA TO FLORIDA. Three specimens, 81–107 mm, COMBAT St. 385, 34°46′N, 75°37′W, 50 fms., June 17, 1957, BLBG; 2, 103 and 107 mm, COMBAT St. 386, 34°45′N, 75°38′W, 45 fms., June 17, 1957, BLBG; 1, 63 mm, PELICAN St. 192-7, 33°59′N, 76°29′W, 25 fms., March 6, 1940, USNM; 5, 71–84 mm, Pelican St. 195-6, 31°57′N, 79°29′W, 37 fms., March 13, 1940, USNM; 20, 60–102 mm, Pelican St. 179-7, 31°36′N, 79° 43′W, 40 fms., Feb. 1940, USNM; 2, 50 and 69 mm, Pelican St. 179-1, 31°24′N, 80°01′W, 23 fms., Feb. 1, 1940, USNM; 1, 66 mm, Pelican St. 178-18, 31°23′N, 80°04′W, 22 fms., Jan. 31, 1940, USNM; 2, 77 and 108 mm, Pelican St. 198-1, 31°00′N, 80°01′W, 40 fms., March 15, 1940, USNM; 1, 77 mm, Combat St. 353, 30°24′N, 80°20′W, 24 fms., June 3, 1957, BLBG; 1, 89 mm, Pelican St. 177-3, 30°31′N, 80°15′W, 23 fms., Jan. 25, 1940, USNM; 1, 74 mm, Pelican St. 200-10, 30°21′N, 80°36′W, 19 fms., March 27, 1940, USNM; 3, 62–69 mm, Pelican St. 200-11, 30°17′N, 80°27′W, 21 fms., March 27, 1940, USNM; 1, 77 mm, Combat St. 497, 30°13′N, 80°23′W, 25 fms., Aug. 20, 1957, BLBG; 8, 90–120 mm, Silver Bay St. 461, 29°38′N, 80°16′W, 50 fms., June 13, 1958, BLBG; 1, 118 mm, Combat St. 457, 25°16′N, 80°07′W, 65 fms., July 26, 1957, BLBG; 1, 94 mm, Combat St. 455, 25°13′N, 80°10′W, 40–50 fms., July 26, 1957, BLBG.

Gulf of Mexico, and Caribbean Sea to Brazil. Two specimens, 71 and 93 mm, Pelican St. 151-1, 30°14′N, 86°15′W, 15 fms., March 9, 1939, USNM; 1, 79 mm, Pelican St. 153-1, 29°34′N, 85°52′W, 19 fms., March 10, 1939, USNM; 2, 87 and 100 mm, 28°50′N, 85°06′W, 35 fms., March 7, 1954, UF 3599; 1, 50 mm, Pelican St. 86-4, 28°31′N, 91°09′W, 17 fms., July 13, 1938, USNM; 1, 90 mm, Pelican St. 86-1, 28°22′N, 91°22′W, 31 fms., July 13, 1938, USNM; 4, 36–52 mm, Pelican St. 85-6, 28°19′N, 91°24′W, 35 fms., July 12, 1938, USNM; 3, 45–65 mm, Pelican St. 84-3, 28°14′N, 91°41′W, 39 fms., July 12, 1938, USNM; 1, 88 mm, Pelican St. 85-4, 28°11′N, 91°24′W, 47 fms., July 12, 1938, USNM; 2, 100 and 104 mm, Silver Bay St. 190, 28°07′N, 95°03′W, 30 fms., Sept. 27, 1957, BLBG; 1, 73 mm, 27°49′N, 96°31′W, Dec. 14, 1950, CNHM 45068; 3, 80–98 mm, Pelican St. 108-10, 27°45′N, 96°13′W, 39 fms., Jan. 23, 1939, USNM; 4, 78–95 mm, Pelican St. 42-2, 27°43′N, 96°44′W, 17 fms., April 22, 1938, USNM; 1, 75 mm, Pelican St. 112-1, 27°15′N, 96°24′W, 80 fms., Jan. 30, 1939, USNM; 6, 74–97 mm, Pelican St. 112-3, 27°13′N, 96°40′W, 42 fms., Jan. 30, 1939, USNM; 6, 88–108 mm, Pelican St. 112-4, 27°13′N, 96°47′W, 33 fms., Jan. 30, 1939, USNM; 1, 86 mm, Pelican St. 113-8, 27°06′N, 96°53′W, 30 fms., Jan. 31, 1939, USNM; 1, 45 mm, Oregon St. 1059, 18°43′N, 93°29′W, 25 fms., May 16, 1954, USNM; 3, 83–112 mm, Oregon St. 2356, 17°33′N, 63°35′W, 125–132 fms., Sept. 25, 1958, BLBG; 2, 50 and 67 mm, Oregon St. 1873, 16°40′N, 82°12′W, 56 fms., Aug. 22, 1957, BLBG; 3, 138–200 mm, Oregon St. 1879, 16°38′N, 81°39′W, 150 fms., Aug. 22, 1957, BLBG; 1, 175 mm, Oregon St. 1868, 16°36′N, 82°37′W, 175 fms., Aug. 21, 1957, BLBG; 3, 90–116 mm, Oregon St. 1866, 16°30′N, 83°30′W, 38 fms., Aug. 21, 1957, BLBG; 8, 78–143 mm, Oregon St. 1865, 16°20′N, 83°20′W, 42 fms., Aug. 21, 1957, BLBG; 1, 78 mm, Oregon St. 1999, 07°55′N, 57°34′W, 43 fms., Nov. 5, 1957, BLBG; 4, 110–115 mm, Oregon St. 2343, 07°34′N, 57°45′W, 19 fms., Sept. 19, 1958, BLBG; 7, 95–190 mm, Oregon St. 2262, 07°18′N, 56°49′W, 30–33 fms., Sept. 1, 1958, BLBG; 1, 147 mm, Oregon St. 2016, 07°18′N, 54°08′W, 50 fms., Nov. 8, 1957, BLBG; 3, 172–198 mm, OREGON St. 2021, 07°18′N, 53°32′W, 100 fms., Nov. 8, 1957, BLBG; 8, 73–130 mm, OREGON St. 2268, 06°53′N, 55′59′W, 23 fms., Sept. 2, 1958, BLBG.

Distinctive Characters. See *Key to Atlantic Species*, p. 48.

Description. Proportional dimensions in per cent of standard length, with ranges given first, followed by the mean in parentheses, based on measurements from 17 specimens: 36, 44, 45, 49, 75, 77, 81, 84, 98, 103, 107, 108, 118, 140, 172, 181, and 200 mm SL.

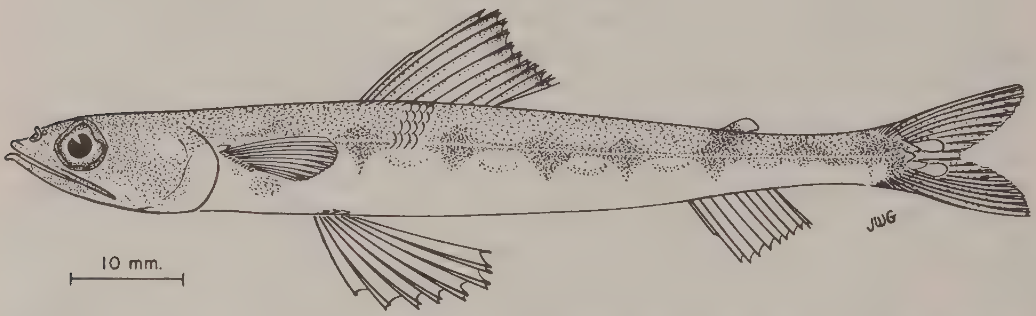

FIGURE 19. *Synodus poeyi*, 81.5 mm SL, off Cape Lookout, North Carolina, COMBAT St. 385, 34°46′N, 75°37′W, 50 fms., BLBG.

Body at base of pelvic fin: depth 8.8–18.5 (12.4); width 5.6–16.0 (11.7).

Head: length 22.1–28.3 (24.9).

Snout: length 2.6–6.5 (4.8).

Eye: diameter 5.0–12.4 (6.6).

Interorbital: width 3.4–5.1 (4.3).

Premaxillary: length 10.7–16.8 (14.0).

Distance from snout to origin of: dorsal fin 37.1–43.0 (40.6); anal fin 71.4–77.4 (74.4); pelvic fin 32.5–40.3 (36.1).

Distance from: origin of dorsal fin to origin of adipose fin 37.5–42.6 (40.4); tip of pectoral fin to origin of pelvic fin 0 to +5.5 (+2.1).

Dorsal fin: length of base 13.2–16.6 (14.8); length of longest ray 13.0–23.3 (17.6); length of last ray 6.1–11.7 (8.1).

Anal fin: length of base 8.3–13.0 (10.8).

Pectoral fin: length of longest ray 11.5–15.8 (13.2).

Pelvic fin: length of first ray 8.4–13.9 (11.1); length of longest ray 14.2–20.4 (18.0).

Counts, based on 106 specimens.

Scales: predorsal 13–16 (29 specimens with 13, 43 with 14, 14 with 15, 2 with 16); rows of complete scales between lateral line and base of dorsal fin 3 (all specimens).

Lateral-line scales: 43–48 (8 with 43, 29 with 44, 22 with 45, 22 with 46, 19 with 47, 3 with 48).[7]

Fin rays: Dorsal fin 10–12 (37 with 10, 65 with 11, 2 with 12); anal fin 9–12 (7 with 9, 74 with 10, 22 with 11, 1 with 12); pectoral fin 10–12 (2 with 10, 64 with 11, 40 with 12).

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[7] Fowler (*24*: 131) gave a low lateral-line scale count of 42+2 for a 43-mm TL specimen.

HEAD depressed; top of head only slightly rugose. SCALES large. LATERAL LINE well marked, with a slight keel on caudal peduncle. SNOUT wide and blunt, shorter than eye diameter on specimens to about 100 mm SL and nearly equal to, or longer than, eye diameter on larger specimens. INTERORBITAL space moderately concave. LOWER JAW extending beyond upper jaw, and ending in a fleshy knob (knob more pronounced in large specimens). DORSAL fin with anterior rays extending to, and usually beyond, tips of some succeeding rays when laid back; its origin about equidistant between adipose fin and tip of snout. ANAL base shorter than dorsal base, its length 59.0–90.1 % of dorsal base length. PECTORAL fin with tip extending beyond origin of pelvic fin, but occasionally just reaching to the origin. PELVIC fin usually with 6th or 7th ray the longest, occasionally the 8th as long as the 6th or 7th. Pelvic bones with posterior processes long, flat, and broad with acute tip and a mid-dorsal ridge diminishing distally.

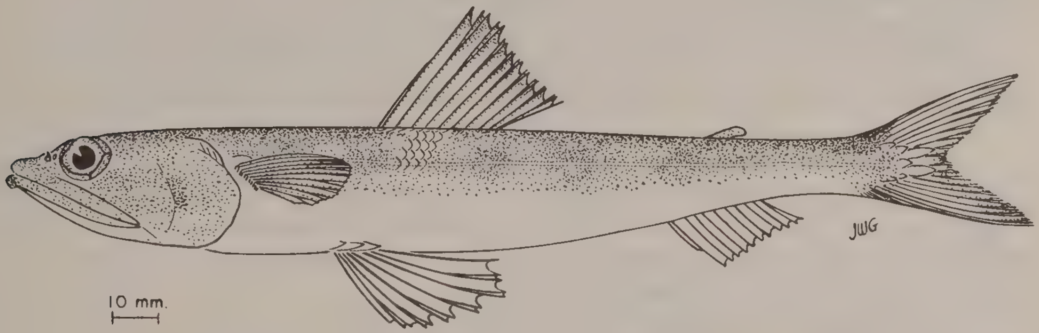

FIGURE 20. *Synodus poeyi*, 198 mm SL, off Surinam, OREGON St. 2021, 07°18′N, 53°32′W, 100 fms., BLBG.

Color. In preservative, adults (Fig. 20) usually greyish brown on head, back, and top half of sides, with about 8 obscure darker blotches on sides along lateral line. Belly and lower part of sides white. Dorsal and pectoral fins uniformly dusky; caudal fin dusky, the inner part of lower lobe much darker than remainder of fin; pelvic and anal fins pale; adipose fin and fleshy knob at tip of lower jaw darkened to almost black. No black blotch on shoulder girdle. Basic coloration similar in young specimens (Fig. 19) except that the blotches along the lateral line are distinct and generally in the form of diamonds.

Four more or less distinct dark crossbars on the back (*60*: 105) and faintly crossbarred dorsal and upper caudal fins (*50*: 21) have been described, but such were not present on our specimens.

Size. The largest specimen examined and the largest yet recorded was 200 mm SL—from 150 fathoms off Honduras. The occurrence records indicate a trend of the smaller specimens to frequent shallower waters and of the larger ones to occupy the deeper waters.

Habits. Apparently this is an offshore bottom species that does not at any size tend to inhabit shore areas. The extensive records from trawling activities of the PELIcan, Oregon, Combat, and Silver Bay indicate a depth distribution from 15[8] to 175 fathoms, but with the majority of records less than 100 fathoms, or within the limits of the Continental Shelf. Off Texas and Mexico, *S. poeyi* was reported to be most abundant at depths greater than 17 fathoms and to move shoreward during the summer (*32*: 290). The depth record for the species is 175 fathoms—a 175-mm specimen from off Honduras.

Nothing has been reported concerning behavior, food, predators, growth, and development except that a sexually mature specimen of 105 mm TL was taken in August off Dry Tortugas, Florida (*50*: 21). Digenetic trematodes have been recorded as parasites (*51*: 339, 375).

Relation to Man. Not occurring inshore, and taken only incidental to other fishing operations in but few areas and then not utilized, the species has no significant value to man.

Relationship to Extralimital Species. Following the key characters and descriptions used by Norman and Matsubara (*60*: 102; *53*: 2), the range of lateral-line scales for *S. poeyi* overlaps the ranges for *S. fuscus* Tanaka and *S. macrops* Tanaka, each with counts of 49–55 lateral-line scales. However, the latter two species do not have the lower jaw ending in a fleshy knob.

S. poeyi averages a greater number of anal rays than *S. marchenae* (8–9 in the latter).

Range. Fig. 18. The species was formerly reported from the West Indies and Atlantic coast of Panama. Present records extend the range along the coast of the United States from North Carolina to lower Florida, across the northern Gulf of Mexico, the lower Gulf of Mexico in the Campeche Bay region, and the Atlantic Ocean off South America south to about 7° N.

Synonyms and References:

Synodus intermedius (*non* Spix), Poey, An. Soc. esp. Hist. Nat., *5* (1), 1876: 143 (descr.; Cuba); Meek, Proc. Acad. nat. Sci. Philad., 1884: 132 (key; descr.; Havana, Cuba); Jordan, Proc. U.S. nat. Mus., *7* (416), 1884: 108 (discuss. nomencl.); Jordan, Proc. U.S. nat. Mus., *9* (593), 1884: 526 (synonym of *S. poeyi* Jordan).

Synodus poeyi Jordan, Proc. U.S. nat. Mus., *9* (593), 1887: 526 (type loc., Havana market, Cuba; types designated from previous descr. of Meek, 1884: 133; holotype deposition unknown; paratype MNHN 87–383, *fide* Bertin and Estève, Impremerie Nat., 6, 1950: 7); Jordan, Proc. U.S. nat. Mus., *9* (595), 1887: 563 (W. Indies); Jordan and Bollman, Proc. U.S. nat. Mus., *12* (770), 1890: 152 (*cf. S. evermanni*); Jordan and Evermann, Rep. U.S. Comm. Fish and Fish. (1895), *21* (5), 1896: 296 (Havana, Cuba); Jordan and Evermann, Bull. U.S. nat. Mus., *47* (1), 1896: 536 (descr.; key); Evermann and Marsh, Bull. U.S. Fish Comm. (1900), *20* (1), 1902: 92 (key); Fowler, Proc. Acad. nat. Sci. Philad., 1911: 566 (*cf. S. dominicensis*); Meek and Hildebrand, Field Mus. nat. Hist., Zool., *15* (1), 1923: 218 (key; descr.; Fox Bay, Colón and Porto Bello, Caribbean Panama); Jordan, Evermann, and Clark, Rep. U.S. Comm. Fish. (1928), App. 10, 1930: 164 (in check list); Norman, Proc. zool. Soc. London, 1935: 103, 105 (key; descr.; synonyms; Havana, Cuba); Whitley, Aust. Zool., *8* (4), 1937: 219 (incl. in proposed n. gen. *Negotirus*); Fowler, Notulae Nat., *35*, 1939: 9 (discuss.); Longley and Hildebrand, Publ. Carnegie Instn. Wash., *34* (535), 1941: 21 (descr.; color; 13–55.5 fms.; *cf. S. intermedius*; Bush Key and Tortugas, Florida); Fowler, Monogr. Acad. nat. Sci. Philad., *6*, 1944: 131, 459 (descr.; Old Providence I., Caribbean, also after Meek and Hildebrand 1923); Manter, Amer. Midl. Nat., *38* (2), 1947: 339, 375 (digenetic trematodes; Tortugas, Florida); Hildebrand, Smithson. misc. Coll., *110* (9), 1948: 12 (*cf. S. cinereus*); Fowler, Notulae Nat., *246*, 1952: 3 (descr.; off Palm Beach, and SW. of Sombrero Key Light near Marathon, Florida); Bertin and Estève, Impremerie Nat., 6, 1950: 7 (paratype reported, MNHN 87–383, 100 mm); Fowler, Mem. Soc. cubana Hist. nat., *21* (1), 1952: 86 (Hispaniola); Fowler, Caldasia, *6* (27), 1953: 51 (Old Providence, Bahamas); Hildebrand, Publ. Inst. mar. Sci. Texas, *3* (2), 1954: 289, 290, 332, 335, 337, 346 (depth; off Corpus Christi Pass, Padre I., St. Joseph I., and Mustang I., Texas); Springer and Bullis, U.S. Fish Wildl. Serv., Sp. Sci. Rep. Fish. 196, 1956: 54 (Oregon Sts., Gulf of Mexico); Briggs, Bull. Fla. St. Mus., Biol. Sci., *2* (8), 1958: 257 (range); Gibbs, Copeia, 1959: 235, fig. 1D (larvae descr.).

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[8] Longley and Hildebrand (*50*: 21) reported a specimen taken from 13 to 15 fathoms off Dry Tortugas.

Synodus dominicensis Fowler, Proc. Acad. nat. Sci. Philad., 1911: 564, fig. 2 (type loc., Santo Domingo, Greater Antilles; holotype, ANSP 15883); Fowler, Copeia, 1915: 50 (Santo Domingo); Norman, Proc. zool. Soc. London, 1935: 105 (*S. dominicensis* synon. with *S. poeyi*); Fowler, Notulae Nat., *35*, 1939: 8 (*cf. S. bondi*); Fowler, Monogr. Acad. nat. Sci. Philad., *6*, 1944: 131 (given as distinct from *S. poeyi*); Fowler, Mem. Soc. cubana Hist. nat., *21* (1), 1952: 86 (Hispaniola).

Saurus poeyi, Metzelaar, Rapp. Bet. Voor. Ind. Zee. Kol. Curaçao, *2* (2), 1919: 23 (probable record for Trinidad).

Questionable Reference:

Synodus poeyi, Borodin, Bull. Vanderbilt Mar. Mus., *1* (1), 1928: 10 (Bahamas; no descr.; no corroborating spec.).

Synodus saurus (Linnaeus) 1758

Lizardfish, Lagarto, Snakefish

Figures 10, 21–23

Study Material. A total of 21 specimens ranging in length between 36 and 226 mm, from: Bahamas. Two specimens, 36 and 46 mm, Rose I., March 25, 1955, ANSP 74962; 2, 46 and 55 mm, N. shore of Hog I., April 14, 1955, ANSP 74963; 2, 116 and 126 mm, N. shore of Hog I., July 6, 1955, ANSP 74965; 1, 92 mm, 1 mi. W. of Cap Cay, July 22, 1955, CNHM 64059; 11, 44–87 mm, N. shore of Rose I., April 3, 1956, ANSP 74966.

Mediterranean Sea. Two specimens, 226 and 95 mm, Bay of Naples, April 1897, USNM 48330, 48331 respect.; 1, 155 mm, Egypt, USNM 167055.

Distinctive Characters. See *Key to Atlantic Species*, p. 48.

Description. Proportional dimensions in per cent of standard length, with ranges given first, followed by the mean in parentheses, based on measurements from 11 specimens: 46, 48, 56, 62, 69, 87, 95, 116, 126, 155, and 226 mm SL.

Body at base of pelvic fin: depth 11.3–15.8 (14.3); width 10.0–15.9 (13.3).

Head: length 23.3–28.7 (25.7).

Snout: length 3.6–6.1 (4.6).

Eye: diameter 3.8–7.1 (5.4).

Interorbital: width 1.1–3.3 (2.4).

Premaxillary: length 10.6–16.1 (14.1).

Distance from snout to origin of: dorsal fin 40.6–44.4 (42.0); anal fin 74.2–78.6 (76.5); pelvic fin 32.9–40.3 (35.6).

Distance from: origin of dorsal fin to origin of adipose fin 39.5–42.6 (41.2); tip of pectoral fin to origin of pelvic fin −0.9 to +3.0 (+1.1).

Dorsal fin: length of base 13.0–14.6

(13.9); length of longest ray 13.0–18.1 (15.2); length of last ray 5.2–7.9 (7.1).

Anal fin: length of base 9.4–12.8 (11.1).

Pectoral fin: length of longest ray 9.6–11.4 (10.4).

Pelvic fin: length of first ray 7.2–11.1 (9.1); length of longest ray 17.6–28.9 (22.6).

Counts based on 20 specimens.

Scales: predorsal 15–20 (1 specimen with 15, 0 with 16, 17 or 18, 9 with 19, 9 with 20); rows of complete scales between lateral line and base of dorsal fin 3 (all specimens).[9]

Lateral-line scales: 55–60 (1 with 55, 2 with 56, 1 with 57, 7 with 58, 6 with 59, 3 with 60), up to 62 reported (*29*: 57).

Fin rays: dorsal fin 11–13 (4 with 11, 14 with 12, 2 with 13); anal fin 9–11 (1 with 9, 14 with 10, 5 with 11), up to 13 reported (*21*: 342; *55*: 9); pectoral fin 12–14 (7 with 12, 12 with 13, 1 with 14).

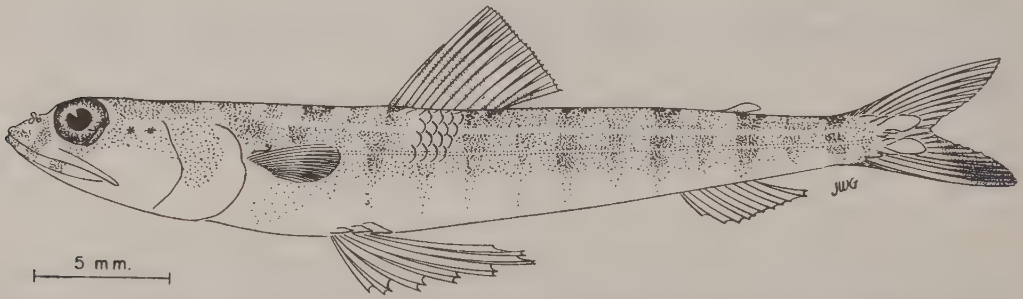

FIGURE 21. *Synodus saurus*, 63.0 mm SL, north shore of Rose Island, Bahamas, St. 276, ANSP 74966.

HEAD but slightly depressed; top of head very rugose. SCALES small. LATERAL LINE not well marked, no keel on caudal peduncle. SNOUT rounded and blunt, usually shorter than eye diameter in small specimens and longer than eye in larger ones (over about 150 mm SL). INTERORBITAL space moderately concave. LOWER JAW included or subequal to upper jaw, not ending in a fleshy knob. DORSAL fin with anterior rays not extending beyond tips of any of succeeding rays when laid back; its origin about equidistant between adipose fin and tip of snout. ANAL base shorter than dorsal base, its length 70.1–89.8 % of dorsal base length. PECTORAL fin with tip extending to origin of pelvic fin or slightly beyond, rarely not extending to pelvic origin. PELVIC fin with 6th ray the longest. Pelvic bones with posterior processes long and narrow, slightly expanded laterally at base with a mid-dorsal ridge diminishing distally.

Color. In preservative, body background color light yellowish grey. Usually about eight moderately broad brownish saddles across back, onto sides, and ending above the lateral line; 1st saddle between bases of pectoral fin, 2nd midway between the first saddle and origin of dorsal fin, 3rd at origin of dorsal fin, 4th at posterior end of dorsal fin, 5th and 6th spaced between posterior end of dorsal fin and adipose fin, 7th at adipose fin, and the 8th between adipose fin and caudal fin (Fig. 22). Narrow brownish saddles between the broader ones (to the adipose fin). In addition, about 7 or 8 prominent brownish blotches along lateral line and less distinct brown blotches between these. Lower part of head, sides of body and belly yellowish white. Dorsal and caudal fins light dusky; other fins clear. This basic coloration more prominent in small individuals (Fig. 21) than in the larger ones examined, in which it has become indistinct.

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[9] Fowler (*21*: 342) gave scale counts for a series of Italian specimens of *S. saurus* that are divergent from other reports and the values we obtained: scales 57 to 66 in lateral line to caudal base, 3 or 4 scales above lateral line, 19 to 21 predorsal scales.

Size. The largest specimen we have examined from the western North Atlantic is 126 mm SL, taken from the north shore of Hog Island, Bahamas. A specimen from Bermuda has been listed as 17 inches long (*28*: 68). A specimen of 445 mm TL (17.5 inches) was recorded from Madeira (*60*: 117).

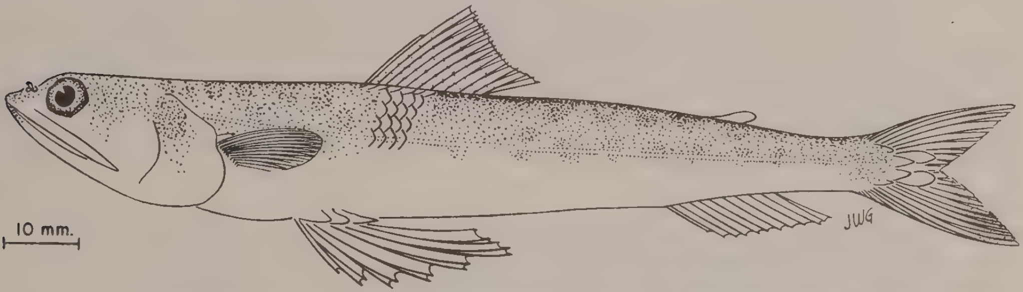

FIGURE 22. *Synodus saurus,* 116 mm SL, north shore of Hog Island, Bahamas, St. 244, ANSP 74965.

Habits. The only sizeable collection of *S. saurus* from the western North Atlantic appears to be the one from the Bahaman shore area made by J. E. Böhlke and C. C. G. Chaplin (deposited in ANSP). This, considered with the absence of specimens from the extensive trawling operations of the vessels PELICAN, OREGON, COMBAT, and SILVER BAY in an area extending along the coast of the United States from North Carolina to Florida, around the Gulf of Mexico, in the Caribbean, and along the coasts of Central and South America to Brazil, indicates that in the western North Atlantic the species apparently does not venture into open ocean areas, or occur other than in the island chains where limited collections have been made.

In the eastern Atlantic and the Mediterranean, *S. saurus* is also known primarily as an insular species, although it has been recorded from continental waters around the Mediterranean periphery and from Atlantic Morocco. Throughout its range it may be regarded as an inhabitant of shallow water. A single deep-water record exists, about 220 fathoms from off Algiers (*18*: 55); but all other recorded depths are of 11 fathoms or less.[10]

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[10] We cannot accredit an unsubstantiated statement by Goode and Bean (*29*: 57) that "It occurs at moderate depths about Bermuda, but probably below the hundred-fathom line."

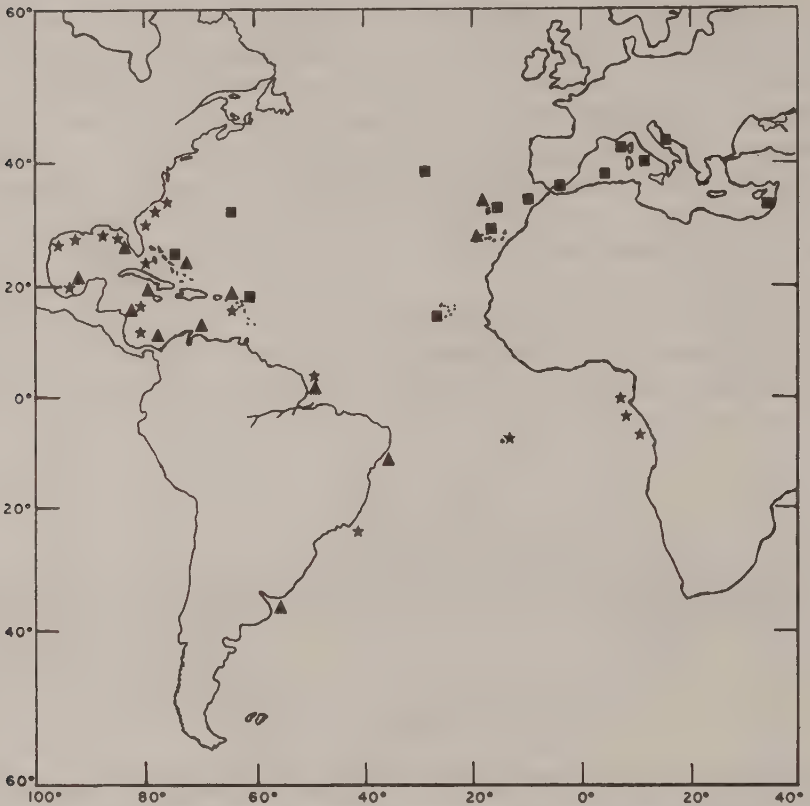

FIGURE 23. Distribution of *Synodus saurus* (squares), *Synodus synodus* (triangles), and *Saurida brasiliensis* (stars).

Little is known of the behavior,[11] food, or enemies of this species. Trematodes have been recorded as parasites (*46*: 86, 105).

Relation to Man. This species is of no significant importance to man. One large specimen has been reported caught on hook and line (*28*: 68).

Relationship to Extralimital Species. Based on descriptions by Norman (*60*), Matsubara (*53*), and Schultz (*69*), and our determinations, *Synodus saurus* is similar to six Indo-Pacific species (*S. indicus*, *S. kaianus*, *S. fuscus*, *S. hoshinonis*, *S. macrops*, and *S. binotatus*) in having 3 rows of complete scales between the lateral line and the mid-dorsal fin base. The remaining Indo-Pacific species have 4–7 such rows. *S. saurus* tends to have more lateral-line scales than *S. fuscus* and *S. macrops* (55–62 in *S. saurus*; 49–55 reported for *S. fuscus* and *S. macrops*). *S. saurus* appears to have a shorter snout and a shorter pectoral fin than *S. hoshinonis* and *S. binotatus* (in *saurus*, snout 3.6–6.1 and pectoral 9.6–11.4 $^0/_0$ of SL; in *hoshinonis*, snout about 9.1–9.8 $^0/_0$ and pectoral about

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[11] Barbour (3: 113) described behavior of fish in shallow water at Bermuda and identified them as this species; but his identifications presumably were by sight only, and he indicated no knowledge of the other species of lizardfish that are common at Bermuda.

11.8–12.4 %; in *binotatus*, snout 6.7–7.7 % and pectoral 12.4–13.0 %). *S. saurus* differs from *S. kaianus* in having a shorter pectoral fin that usually extends only to the pelvic origin (in *S. kaianus*, pectoral about 11.6–12.8 % of SL and extending beyond pelvic base). Differentation of *S. saurus* from *S. indicus* on the basis of published data of the latter is difficult. *S. saurus* averages a larger number of anal and pectoral rays than *S. marchenae* (8–9 and 11–12, respectively, in *S. marchenae*).

Synonymy. Hildebrand (*34*: 10, fig. 5) described *Synodus cinereus* from two specimens taken in the Bahamas (type, 108 mm SL, USNM 53079; paratype, 61 mm SL, USNM 53078); comparison of these with *Synodus saurus* from the Bahamas leaves no doubt that they are identical. Twenty specimens of *S. saurus* have an anal ray range of 9 to 11, with 10 the most frequent count; Hildebrand gave 9 as the anal ray count for his two specimens, but the type actually has 10. Hildebrand indicated that *S. cinereus* also differs from *S. saurus* in the absence of tentacles behind the anterior nostrils; but these are present and entire in the paratype and present but damaged (partly torn away) in the type. We place *S. cinereus* in synonymy with *S. saurus*.

Range. Fig. 23. This species occurs on both sides of the Atlantic. On the western side it has been taken from Bermuda, the Bahamas, and the Leeward Islands, West Indies. Lack of records other than those for the outlying islands off the coasts of the southern United States and northern South America suggests a very specialized habitat.

Synonyms and References:

Salmo saurus Linnaeus, Syst. Nat., ed. 10, 1758: 310 (descr. based on Artedi; type loc. Mediterranean; no type spec. known); Linnaeus, Syst. Nat., ed. 12, *1*, 1766: 511 (Europe); Gmelin, Syst. Nat., *1* (3), 1789: 1476 (after Linnaeus 1766); Bloch, Naturg. ausland. Fische, *8*, 1794: 116, pl. 384, fig. 1 (part; w. Antilles and Mediterranean; excl. Red Sea ref.); Swainson, Nat. Hist. Fish. Amphib. Rept., *2*, 1838: 242 (type of *Laurida* Swainson); Valenciennes *in* Cuvier and Valenciennes, Hist. Nat. Poiss., *22*, 1849: 463 (discuss.); Moreau, Hist. Nat. Poiss., *3*, 1881: 515 (abundant, Mediterranean coast, e. France); Whitley, Aust. Zool., *8* (4), 1937: 119 (as type species of proposed resurrected genus *Tirus* Rafinesque).

Osmerus saurus, Lacépède, Hist. Nat. Poiss., *5*, 1803: 229 (descr.), 235 (listed, based on Linnaeus).

Stolephorus risso Risso, Carett. n. gen., 1810: 56 (type loc., Nice, France; type not known).

Osmerus fasciatus Risso, Ichthyol. Nice, 1810: 326 (type loc. Nice, France; holotype, MNHN B.851, 210 mm; *fide* Bertin and Estève, Impremeria Nat., *6*, 1950: 5); Valenciennes *in* Cuvier and Valenciennes, Hist. Nat. Poiss., *22*, 1849: 470 (ref.; Nice, France); Bertin and Estève, Impremeria Nat., *6*, 1950: 5 (holotype reported in Paris Mus.).

Tirus marmoratus Rafinesque, Carett. n. gen., 1810: 56 (type loc. Palermo, Italy; type spec. not designated).

Saurus saurus, Cuvier, Règne Anim., *1*, 1817: 169 (Mediterranean); Cuvier, Règne Anim., ed. 2, *2*, 1829: 314 (after Cuvier 1817); Griffith, Anim. Kingd., 1834: 430 (after Cuvier 1829); Valenciennes, Poiss., *in* Règne Anim., ed. 3, *2*, 1837: 268 (after Cuvier 1829); Roule, Résult. Camp. Sci. Monaco, *2* (52), 1919: 33 (Villafranca, Azores), 130 (listed), 145 (Povoacao, Azores); Valliant, Résult. Camp. Sci. Monaco, *2* (52), 1919: 130 (Povoacao, Azores).

Alpismaris risso Risso, Hist. Nat. Europe Merid., *3*, 1826: 458 (Nice, France; very young; type spec. not known).

Saurus fasciatus, Risso, Hist. Nat. Europe Merid, *3*, 1826: 464 (Nice, France); Valenciennes *in* Cuvier and Valenciennes, Hist. Nat. Poiss., *22*, 1849: 470 (Nice, France); Moreau, Hist. Nat. Poiss., *3*, 1881: 512, fig. 204 (descr.; synonymy; Nice, Toulon, Marseille, and Mediterranean Sea); Apostolides, Peche en Grece, 1883: 32 (Greece; *fide* Hoffman and Jordan, Proc. Acad. nat. Sci. Philad., 1892: 244); Bertin and Estève, Impremeria Nat., *6*, 1950: 5 (holotype reported in Paris Mus.).

Saurus vulgaris Cloquet, Ichthyol. *in* Dict. Sci. Nat., *22*, 1827: 454 (synonymy *fide* Norman, Proc. zool. Soc. London, 1935: 115).

Saurus trivirgatus Valenciennes *in* Barker-Webb and Berthelot, Hist. Nat. Canaries, Ichthyol., *2* (2), 1835: 72, pl. 15, fig. 1 (type loc. Canary Is.; holotype MNHN A. 8608, 210 mm; *fide* Bertin and Estève 1950: 6); Guichenot, Explor. Alger. Pen. Ann. (1840–42), Sci. Phys., Zool., Poiss., *5*, 1850: 98 (Algiers); Valenciennes *in* Cuvier and Valenciennes, Hist. Nat. Poiss., *22*, 1949: 470 (conclude *S. trivirgatus* a var. of *S. lacerta* Risso); Johnson, Proc. zool. Soc. London, 1863: 42 (ref.; Madeira); Steindachner, Sitz. Akad. Wiss. Wien, *51* (1), 1865: 403 (Santa Cruz de Tenerife, Canary Is.); Sampaio, Mem. Sobre Ilha Terceira, Peixes, 1904 (ref.; *fide* Collins, Acoreana, *5* (2), 1954: 114); Bertin and Estève, Impremeria Nat., *6*, 1950: 6 (holotype reported in Paris Mus.).

Laurida mediterranea Swainson, Nat. Hist. Fish. Amphib. Rept., *2*, 1838: 246 (Mediterranean; subst. name for *Salmo saurus* Linnaeus).

Saurus griseus Lowe, Trans. zool. Soc. London, *2* (3), 1839: 188 (type loc., Madeira; type spec. not designated): Lowe, Proc. zool. Soc. London, *2* (14), 1841: 188 (descr.; Madeira); Costa, Fauna Regno Napoli, 1850: *3* (ref. *fide* Tåning, Rep. Danish oceanogr. Exped. [1908–1910] Medit., *5*, 1918: 3); Johnson, Proc. zool. Soc. London, 1863: 42 (ref.; *S. griseus* Lowe not distingu. from *S. lacerta*); Günther, Cat. Fishes Brit. Mus., *5*, 1864: 395 (descr.; Madeira; Naples, Italy); Steindachner, Sitz. Akad. Wiss. Wien, *57* (1), 1868: 728 (62), pl. 6, fig. 2 (descr.; Santa Cruz de Tenerife, Canary Is.; Malaga, Spain; Madeira Is.); Goode, Bull. U.S. nat. Mus., 5, 1876: 68 (ref.; *S. griseus* a synonym of *S. lacerta* Valenciennes); Bean, Proc. U.S. nat. Mus., *2* (63), 1879: 32 (spec. in USNM from Brit. Mus.); Giglioli, Regio Ist. Studi Sup. Firenze, 1880: 40 (Lesina, Cagliari, and Naples; Stromboli and Lipari, Lipari I.; Messina, Italy); Vinciguerra, Ann. Mus. Storia nat. Genova, *18*, 1883: 571 (Santa Cruz de Tenerife, Canary Is.; Madeira; *fide* Norman, Proc. zool. Soc. London, 1935: 115); Meek, Proc. Acad. nat. Sci. Philad., 1884: 135 (ref.; *S. griseus* synonym of *S. saurus* Linnaeus 1758); Vinciguerra, Atti Soc. Ital. Sci. nat. (1892), *34*, 1893: 329 (Canary Is.); Carus, Prodr. Fauna Medit., *2*, 1893: 561 (Mediterranean); Jeude, Mus. Hist. nat. Pays-Bas, *10* (2), 1898: 30 (listed); Sanzo, Mem. R. Com. talassogr. Ital., *49*, 1915: 1, fig. I (eggs and larva descr.); Tåning, Rep. Danish oceanogr. Exped. [1908–10] Medit., *5*, 1918: 3, fig. 1 (postlarvae; 33°11′N, 21°44′E and 37°52′N, 23°09′E in e. Mediterranean), 149 (postlarvae; 18°00′N, 64°48′W and 17°49′N, 64°51′W in W. Indies n. of St. Croix); Metzelaar, Rapp. Bet. Voor. Ind. Zee. Kol. Curaçao, *2* (2), 1919: 213 (ref.); Breder, Zoologica, N.Y., *29* (1), 1944: 13 (ref.).

Saurus lacerta (*non* Risso), Lowe, Proc. zool. Soc. London, *2* (14), 1841: 188 (descr.; Madeira); Valenciennes *in* Cuvier and Valenciennes, Hist. Nat. Poiss., *22*, 1849: 463 (descr.; Toulon, France; Corsica; Naples, Messina, Sicily, Italy; Athens, Greece); Guichenot, Explor. Alger. Pen. Ann. (1840–42), Sci. Phys., Zool., Poiss., *5*, 1850: 97 (descr.; Algiers); Johnson, Proc. zool. Soc. London, 1863: 41 (ref.; Madeira); Kolombatovic, Godisnje Izv. C. L. Vel. Real Splitu, 1881: 21 (Zirona and Solta Is., Yugoslavia); Raffaele, Mitt. zool. Sta. Neapel, *8*, 1888: 28 (ovarian eggs descr.; Naples; *fide* Delsman, Treubia, 16, 1938: 415); Sanzo, Mem. R. Com. talassogr. Ital., *49*, 1915: 1 (ref.; devel. stages; Mediterranean); Bertin and Estève, Impremeria Nat., *6*, 1950: 6 (syntypes of Cuvier and Valenciennes in Paris Mus.); Nair, Proc. Indian Acad. Sci., (B) *35* (5), 1952: 199 (ref.; Bangalore).

Synodus lacerta (*non* Risso), Goode, Bull. U.S. nat. Mus., *1* (5), 1876: 12, 14, 68 (descr.; Bermuda); Bean, Field Columbian Mus., Zool. (Publ. 108), *7* (2), 1906: 35 (ref.).

Synodus saurus, Meek, Proc. Acad. nat. Sci. Philad., 1884: 135 (key; synonymy); Jordan, Proc. U.S. nat. Mus., *9* (593), 1887: 526 (*cf. S. foetens*); Jordan, Proc. U.S. nat. Mus., *9* (595), 1887: 563 (W. Indies); Hoffman and Jordan, Proc. Acad. nat. Sci. Philad., 1892: 244 (Greece); Goode and Bean, Sp. Bull. U.S. nat. Mus., 2, 1895: 57 (descr.; Bermuda); Jordan and Evermann, Rep. U.S. Comm. Fish and Fish. (1895), *21* (5), 1896: 296 (s. European seas; Medit.; Bermuda); Jordan and Evermann, Bull. U.S. nat. Mus., *47* (1), 1896: 537 (descr.; key); Jordan and Gunn, Proc. Acad. nat. Sci. Philad., 1898: 340 (Canary Is.); Evermann and Marsh, Bull. U.S. Fish Comm. (1900), *20* (1), 1902: 92 (key); Schreiner and Miranda Ribeiro, Arch. Mus. nac. Rio de J., *12*, 1903: 105 (Procedencia?); Gill, Proc. U.S. nat. Mus., *26* (1344), 1903: 962 (discuss.); Barbour, Bull. Mus. comp. Zool. Harvard, *46* (7), 1905: 113 (habits; Flatts Inlet and Cooper's I., Bermuda); Bean, Field Columbian Mus., Zool. (Publ. 108), *7* (2), 1906: 35 (listed after Bean 1877 and Barbour 1905); Pietschmann, Ann. Naturh. Hofmus., Wien, *21*, 1906: 134 (descr.; Atlantic off Morocco); Linton, Proc. U.S. nat. Mus., *33* (1560), 1907: 86, 105 (trematode parasites; Bermuda); Fowler, Proc. Acad. nat. Sci. Philad., 1911: 563 (Italy); Buen, Cat. Ict. Medit. Espan. Marruccos, 1926: 50 (ref. *fide* Norman, Proc. zool. Soc. London, 1935: 115); Arambourg, Mat. Carte Géol. Algérie, Paléont., (1) 6, 1927: 37 (descr.; *cf.* fossil *Synodus avus*); D'Erasmo, Atti Accad. Sci. fis. Mat. Napoli, (2) *18*, 1930: 38 (ref.); Jordan, Evermann, and Clark, Rep. U.S. Comm. Fish. (1928), App. 10, 1930: 163 (in check list); Norman, Proc. zool. Soc. London, 1935: 100, fig. 1A (young ill. after Sanzo, Mem. R. Com. talass. Ital.. *49*, 1915), 103 (key), 115 (synonymy in part, excl. unqualified ref. to Beebe and Tee-Van, Zoologica, N.Y., *13* (7), 1933; descr.; Naples, Italy; Nice, France; Cyprus; Jaffa, Palestine; Great Salvage I., Madeira; St. Vincent, Cape Verde Is.; Saba, Leeward Is.); Fowler, Bull. Amer. Mus. nat. Hist., *70* (1), 1936: 343, fig. 160 (key; descr.; synonymy; Fayal, Azores; Italy); Fowler, Bull. Amer. Mus. nat. Hist., *70* (2), 1936: 1219 (Santa Cruz, Canaries); Breder, Zoologica, N.Y., *29* (1), 1944: 13 (metamorphosis); Maul, Bol. Mus. Mun. Funchal, *2* (2), 1946: 9, fig. 1 (descr.; Funchal market, Madeira); Lozano Rey, Mem. R. Acad. Cien. Madrid, *11*, 1947: 379, fig. 15, pl. 6, fig. 2 (larva ill.; descr.; Malaga and Vinaroz, Spain; Majorca and Mahon, Balearic Is., Mediterranean); Hildebrand, Smithson. misc. Coll., *110* (9), 1948: 13 (*cf. S. cinereus*); Maul *in* Noronha and Sarmento, Peixes, Madeira, ed. 2, 1948: 142 (Madeira); Ben-Tuvia, Bull. Israel Dept. Fish., Sea Fish. Res. Sta., *8*, 1953: 7 (Mediterranean Israel); Collins, Acoreana, *5* (2), 1954: 55 (Azores); Dieuzeide and Novella, Bull. Sta. Aquic. Pêche Castiglione, *5*, 1954: 55, text-fig. (descr.; coast of Algiers and Golfe de Genes, Algeria); Dollfus, Trav. Inst. sci. Chérifien, Zool., *6*, 1955: 37 (possible occur. off Morocco); Klausewitz, Erge. Galapagos-Exped. 1953/54 Inst. Sub. Fors., Vaduz, *39* (1/2), 1958: 58, fig. 1 (descr.; Sao Miguel, Azores); Gibbs, Copeia, 1959: 253, fig. 1 c (larvae descr.).

Trachinocephalus myops (*non* Forster), Bean, Fish. Bahama Is., 1905: 297 (Clarence Harbor and near Nassau, Bahamas); Hildebrand, Smithson. misc. Coll., *110* (9), 1948: 12 (ref. to Bean 1905: 297 misident.; spec. designated types of *Synodus cinereus*).

Saurus (*Synodus*) *saurus*, Metzelaar, Rapp. Bet. Voor. Ind. Zee. Kol. Curaçao, *2* (2), 1919: 22 (descr.; Well Bay, Saba, Leeward Is.).

Synodus foetens (*non* Linnaeus), Beebe and Tee-Van, Zoologica, N.Y., *13* (7), 1933: 139 (part; records of *S. lacerta* of Goode 1876 and of *S. saurus* of Barbour 1905 and Bean 1906 from Bermuda; excl. ref. to *S. foetens* from U.S. coast).

Aulopus filamentosus (*non* Cloquet), Nobre, Fauna Marinha Portugal Vert., *1*, 1935: 395 (synonymy only, in part; ref. to *Saurus lacerta* of Lowe 1841 and of Noronha and Sarmento 1934).

Synodus cinereus Hildebrand, Smithson. misc. Coll., *110* (9), 1948: 10, fig. 5 (type loc. Clarence Harbor and an island near Nassau, Bahama Is.; type and paratype USNM 53079 and 53078); Springer and Bullis, U.S. Fish Wildl. Serv., Sp. Sci. Rep. Fish. 196, 1956: 54 (by OREGON on Bahama Bank 1 m. w. of Cat Cay); Gibbs, Copeia, 1959: 232 (ref.).

Questionable References:

Saurus lacerta (*non* Risso?), Bonaparte, Cat. Pesci Europei, 1846: 35 (listed; *Laurida mediterranea* Swainson in synonymy).

Laurus viridis Poggi y Borsotto, Guia Hist.-Descr. Santa Cruz de Tenerife, 1881: 35 (Santa Cruz de Tenerife, Canary Is.; *fide* Fowler, Bull. Amer. Mus. nat. Hist., *70* (1), 1936: 343).

Elops lacerta (*non* Risso), Pellegrin, Bull. Soc. zool. Fr., *38*, 1913: 151, 152, 154 (Conakry, Guinea, Fr. W. Africa; Ivory Coast; Libreville, Gabon, Fr. Equatorial Africa; cited as *Elops lacerta* Cuvier and Valenciennes with no descr.).

Negative References:

Not *Osmerus saurus* (Linnaeus), Risso, Ichthyol. Nice, 1810: 325 (descr. of *Aulopus filamentosus* (Cloquet); holotype of *O. saurus* Risso, MNHN B 850; *fide* Bertin and Estève, Impremeria Nat., *6*, 1950: 5).

Not *Saurus lacerta* Risso, Hist. Nat. Europe Mérid., *3*, 1826: 463 (descr. of *Aulopus filamentosus* Cloquet).

Synodus foetens (Linnaeus) 1766

Lizardfish, Sand pike, Lagarto

Figures 9, 24–26

Study Material. A total of 293 specimens ranging in length between 30 and 405 mm, from: ATLANTIC COAST OF THE UNITED STATES, NORTH CAROLINA TO FLORIDA. Four specimens, 205–265 mm, COMBAT ST. 377, 35°00′N, 75°30′W, 25 fms., June 17, 1957, BLBG; 5, 165–202 mm, Combat St. 378, 34°58′N, 75°32′W, 30 fms., June 17, 1957, BLBG; 3, 135–220 mm, from Beaufort, North Carolina, June 19, 1956, UF 5239; 1, 100 mm, Pelican St. 187-1, 34°16′N, 76°24′W, 17 fms., Feb. 27, 1940, USNM; 1, 181 mm, Pelican St. 187-2, 34°11′N, 76°18′W, 22 fms., Feb. 27, 1940, USNM; 1, 225 mm, Pelican St. 185-1, 33°33′N, 76°49′W, 75–100 fms., Feb. 16, 1940, USNM; 2, 120–129 mm, Pelican St. 194-5, 32°58′N, 78°56′W, 10 fms., March 9, 1940, USNM; 2, 260–275 mm, Combat St. 283, 32°56′N, 78°06′W, 50 fms., April 19, 1957, BLBG; 1, 132 mm, Pelican St. 182-23, 32°51′N, 78°59′W, 14 fms., Feb. 12, 1940, USNM; 1, 111 mm, Pelican St. 180-3, 31°50′N, 80°25′W, 11 fms., Feb. 2, 1940, USNM; 1, 290 mm, Combat St. 511, 31°36′N, 79°38′W, 50 fms., Oct. 3, 1957, BLBG; 1, 220 mm, Pelican St. 178-18, 31°23′N, 80°04′W, 22 fms., Jan. 31, 1940, USNM; 1, 141 mm, coastal Georgia, fall of 1932, USNM.

From the outer beaches on St. Simons I., Georgia: 1, 33 mm, May 4, 1954; 19, 30–44 mm, May 28, 1956; 3, 36–62 mm, June 11, 1956; 1, 165 mm, June 26, 1956; 1, 57 mm, Nov. 6, 1956; 2, 36 and 41 mm, April 27, 1957; 3, 34 mm, May 16, 1957; 10, 35–73 mm, May 31, 1957; all BLBG.

From the commercial trawling area off Brunswick, Georgia (principally 2–6 fms.): 2, 240 and 243 mm, Aug. 17, 1955; 5, 160–335 mm, Oct. 13, 1955; 9, 165–338 mm, Oct. 20, 1955; 7, 155–320 mm, Oct. 23, 1955; 3, 167–204 mm, Nov. 22, 1955; 2, 308 and 310 mm, 1955; 1, 152 mm, May 17, 1956; 11, 141–247 mm, May 16, 1957; 2, 185 and 195 mm, June 26, 1957; 2, 140 and 190 mm, Aug. 14, 1957; 11, 137–278 mm, July 21, 1958; all BLBG.

One specimen, 97 mm, Pelican St. 176-10, 30°29′N, 80°33′W, 20 fms., Jan. 25, 1940, USNM; 1, 255 mm, Combat St. 496, 30°16′N, 80°21′W, 25 fms., Aug. 20, 1957, BLBG; 8, 245–350 mm, Combat St. 497, 30°13′N, 80°23′W, 25 fms., Aug. 20, 1957, BLBG; 2, 108 and 110 mm, Pelican St. 174-15, 29°56′N, 81°07′W, 11 fms., Jan. 20, 1940, USNM; 2, 250 and 395 mm, Combat St. 488, 29°30′N, 80°13′W, 50 fms., Aug. 19, 1957, BLBG; 1, 250 mm, Combat St. 490, 29°29′N, 80°10′W, 100 fms., Aug. 19, 1957, BLBG; 19, 158–321 mm, Combat St. 339, 29°19′N, 80°18′W, 25 fms., June 1, 1957, BLBG; 1, 230 mm, Combat St. 336, 29°10′N, 80°19′W, 25 fms., June 1, 1957, BLBG; 2, 239 and 270 mm, Combat St. 341, 29°10′N, 80°20′W, 22 fms., June 1, 1957, BLBG; 29, 192–345 mm, Combat Sts. 333–334, 28°58′N to 29°15′N, 80°13′W, 30 fms., June 1, 1957, BLBG; 1, 150 mm, Pelican St. 211-3, 29°09′N, 80°52′W, 10 fms., April 5, 1940, USNM; 8, 207–355 mm, Combat St. 321, 29°09′N, 80°41′W, 13 fms., April 30, 1957, BLBG; 4, 249–295 mm, Combat St. 335, 29°03′N, 80°13′W, 28 fms., June 1, 1957, BLBG; 23, 185–320 mm, Combat St. 333, 28°58′N, 80°13′W, 30 fms., June 1, 1957, BLBG; 1, 158 mm, Pelican St. 209-3, 28°58′N, 80°45′W, 11 fms., April 5, 1940, USNM; 1, 200 mm, Cape Canaveral, Florida, USNM; 2, 180–185 mm, Pelican St. 169-3, 28°23′N, 80°23′W, 9 fms., Jan. 18, 1940, USNM; 1, 255 mm, Theodore N. Gill Cruise 2, St. 10, 28°18′N, 80°10′W, 20 fms., April 24, 1953, BLBG; 11, 193–405 mm, Combat St. 320, 28°17′N, 80°08′W, 25 fms., April 28, 1957, BLBG; 1, 31 mm, Jupiter Inlet near Palm Beach, Florida, April 4, 1958, UF 7109; 8, 52–140 mm, Inland Waterway, 4.5 mi. N. of Jupiter Inlet, Florida, April 20, 1957, UF 5189; 1, 105 mm, Silver Bay St. 498, 27°28′N, 80°14′W, 4–6 fms., June 23, 1958, BLBG; 1, 35 mm, 1 mile W. of mouth of St. Lucie Inlet, Florida, March 5, 1958, UF 5188.

Gulf of Mexico, and Caribbean Sea to Brazil. Two specimens, 175 and 265 mm, Pascagoula, Mississippi, Jan. 1956, BLBG; 1, 197 mm, Callou Bay, Louisiana, July 16, 1930, USNM; 3, 95–210 mm, off Freeport, Texas, Sept. 1947, USNM; 1, 166 mm, Oregon St. 944, 29°50′N, 86°30′W, 50 fms., March 21, 1954, UF 5193; 2, 220 and 246 mm, Silver Bay St. 174, 29°43′N, 88°11′W, 21 fms., Aug. 29, 1957, BLBG; 1, 200 mm, Silver Bay St. 327, 29°08′N, 88°40′W, 50 fms., March 25, 1958, BLBG; 1, 254 mm, Pelican St. 77-3, 29°04′N, 89°36′W, 8 fms., July 8, 1938, USNM.

From Cedar Keys, Florida: 1, 63 mm, inside Seahorse Key and around Snake Key, Aug. 18–20, 1949, UF 7110; 3, 89–119 mm, Grassy Keys, April 17, 1950, UF 5192; 1, 130 mm, NW. side of Seahorse Key, June 28, 1953, UF 5240; 1, 126 mm, deep flats near North Key, July 12, 1953, UF 5244; 2, 170 and 225 mm, NW. side of Seahorse Key, July 25, 1953, UF 5242; 1, 213 mm, N. edge of main channel, Aug. 16, 1953, UF 7112; 1, 186 mm, deep flats on W. side of North Key, Sept. 6, 1953, UF 7111; 2, 41 and 61 mm, from main ship channel, Oct. 18, 1953, UF 5241; 3, 109–144 mm, flats and channels around Seahorse Key, 1952, UF 5190.

Two specimens, 212 and 230 mm, Pelican St. 66-7, 28°59′N, 91°48′W, 8 fms., May 11, 1938, USNM; 1, 158 mm, SW. of Eugine Light Beacon, Louisiana, 11 fms., May 21, 1941, USNM; 1, 129 mm, Pelican St. 81-5, 28°45′N, 91°17′W, 8 fms., July 11, 1938, USNM; 1, 215 mm, Silver Bay St. 190, 28°07′N, 95°03′W, 30 fms., Sept. 27, 1957, BLBG; 1, 270 mm, Silver Bay St. 181, 28°04′N, 92°05′W, 43 fms., Sept. 22, 1957, BLBG; 1, 253 mm, Silver Bay St. 281, 27°45′N, 95°46′W, 40 fms., Feb. 2, 1958, BLBG; 1, 262 mm, Oregon St. 1048, 21°17′N, 91°18′W, 20 fms., May 13, 1954, USNM; 2, 185 and 230 mm, Oregon St. 1048, 21°17′N, 91°18′W, 20 fms., May 13, 1954, UF 5195; 1, 181 mm, Oregon St. 446, 20°05′N, 91°28′W, 17 fms., Aug. 26, 1951, USNM; 1, 196 mm, Oregon St. 1060, 18°43′N, 93°30′W, 35 fms., May 16, 1954, UF 5199; 1, 230 mm, Oregon St. 1934, 16°00′N, 82°05′W, 21 fms., Sept. 15, 1957, BLBG; 1, 270 mm, Oregon St. 1935, 15°57′N, 82°06′W, 21 fms., Sept. 15, 1957, BLBG; 1, 235 mm, Oregon St. 2262, 07°18′N, 56°49′W, 30–33 fms., Sept. 1, 1958, BLBG; 2, 217 and 270 mm, Oregon St. 2268, 06°53′N, 55°59′W, 23 fms., Sept. 2, 1958, BLBG; 1, 165 mm, Oregon St. 2091, 00°33′N, 47°03′W, 20 fms., Nov. 18, 1957, BLBG; 1, 243 mm, Kingston Harbor, Jamaica, June 9, 1958, UF 5191.

Distinctive Characters. See *Key to Atlantic Species*, p. 48.

Description. Proportional dimensions in per cent of standard length, with ranges given first, followed by the mean in parentheses, based on measurements from 20 specimens: 36.5, 40, 54, 60, 73, 110, 120, 129, 141, 158, 167, 181, 197, 222, 248, 265, 287, 320, 345, and 405 mm SL.

Body at base of pelvic fin: depth 9.8–14.4 (11.7); width 9.3–14.3 (12.4).

Head: length 20.6–26.3 (23.6).

Snout: length 4.4–8.0 (6.0).

Eye: diameter 3.4–6.2 (4.2).

Interorbital: width 2.8–5.4 (3.9).

Premaxillary: length 11.7–16.2 (13.8).

Distance from snout to origin of: dorsal fin 42.5–48.8 (44.1); anal fin 73.8–78.0 (75.3); pelvic fin 34.4–40.0 (36.8).

Distance from: origin of dorsal fin to origin of adipose fin 33.1–39.0 (36.2); tip of pectoral fin to origin of pelvic fin −4.2 to 0 (−1.8).

Dorsal fin: length of base 10.6–12.5 (11.4); length of longest ray 9.9–16.2 (14.3); length of last ray 3.8–7.5 (6.3).

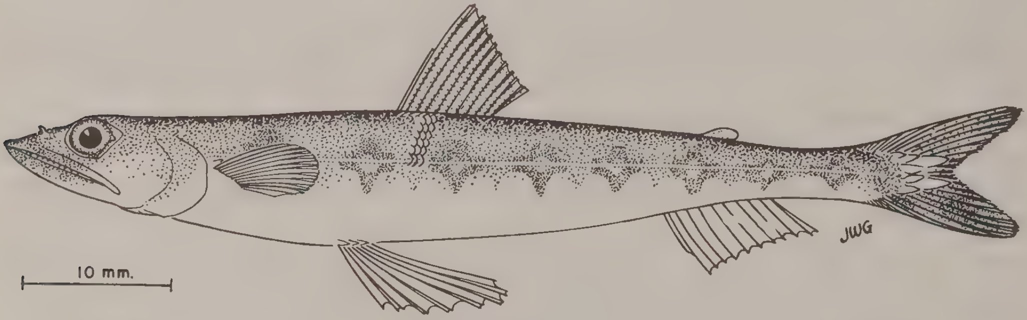

FIGURE 24. *Synodus foetens*, 57.0 mm SL, East Beach, St. Simon Island, Georgia, BLBG.

Anal fin: length of base 9.0–13.9 (12.8).

Pectoral fin: length of longest ray 9.5–12.8 (11.2).

Pelvic fin: length of first ray 8.0–9.9 (8.9); length of longest ray 15.8–21.3 (18.2).

Counts based on 282 specimens.

Scales: predorsal 20–30 (1 specimen with 20, 4 with 21, 11 with 22, 24 with 23, 27 with 24, 33 with 25, 37 with 26, 36 with 27, 31 with 28, 27 with 29, 6 with 30);[12] rows of complete scales between lateral line and base of dorsal fin 4–6 (33 with 4, 225 with 5, 17 with 6).

Lateral-line scales: 56–65 (3 with 56, 16 with 57, 18 with 58, 29 with 59, 68 with 60, 58 with 61, 53 with 62, 23 with 63, 11 with 64, 1 with 65).

Fin rays: dorsal fin 10–13 (30 with 10, 171 with 11, 78 with 12, 2 with 13)[13]; anal fin 10–14 (2 with 10, 33 with 11, 141 with 12, 102 with 13, 3 with 14); pectoral fin 12–15 (8 with 12, 143 with 13, 130 with 14, 1 with 15).

HEAD depressed; top of head only slightly rugose. SCALES small. LATERAL LINE well marked; no keel on caudal peduncle. SNOUT triangular and moderately sharp, usually longer than eye diameter (slightly shorter or equal to on small specimens, much longer on specimens over 200 mm SL). INTERORBITAL space moderately concave.

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[12] The predorsal scale count of 15–20 given by Norman (*60*: 119) is most probably in error.

[13] Jordan and Evermann (*41*: 538) listed a dorsal-ray count of 9 or 10.

Lower jaw included or subequal to upper jaw, ending in a fleshy tip (but not knoblike as in *S. poeyi*). Dorsal fin with some of anterior rays extending beyond tips of some or all of the succeeding rays when laid back; its origin considerably closer to adipose fin than to tip of snout. Anal fin base usually longer than dorsal base but occasionally shorter, its length 82.5–125.0% of dorsal base length. Pectoral fin with tip not extending to origin of pelvic fin (rarely extending to, or slightly beyond, pelvic origin). Pelvic fin with 6th or 7th ray the longest (usually the 7th). Pelvic bones with posterior processes long and narrow, slightly expanded laterally in proximal fourth and a mid-dorsal ridge diminishing distally.

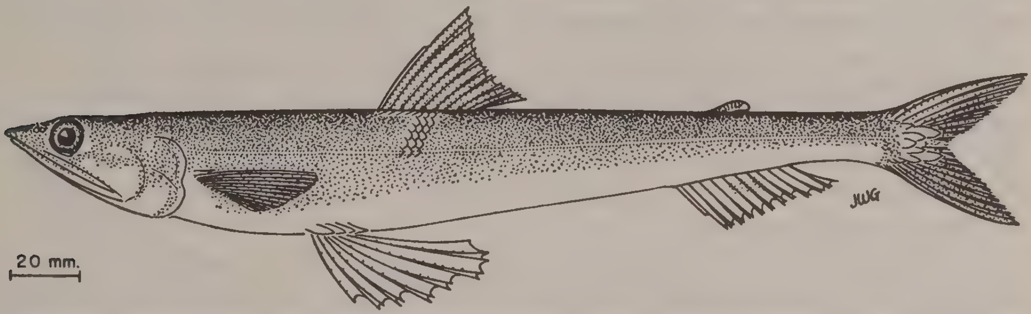

Figure 25. *Synodus foetens*, 255 mm SL, off Jacksonville, Florida, Combat St. 496, 30°16′N, 80°21′W, 25 fms., BLBG.

Color. In preservative, adults (Fig. 25) usually greyish on head, back, and sides, with about eight obscure blotches on the sides in some specimens, but plain in others. Belly white. Dorsal fin with scattered pigment on the rays; caudal fin dusky with blackish margins; anal and pelvic fins with little pigmentation; pectoral fin uniformly dusky; adipose fin with dorsal portion black; young specimens (Fig. 24) with about eight very distinct patches of color arranged as crosses with light centers.

In life, adults with a greenish cast on top and sides; the belly, anal and pelvic fins with a yellowish tinge, this sometimes evident in preserved specimens. Wide variations of color occur in specimens from certain localities. For example, the specimens examined from inside waters near Cedar Keys, Florida, are dark brownish on the top and sides with numerous darker brown blotches; in addition, brownish pigment spots occur on the belly and underside of the head on a yellowish background. The fins are all more heavily pigmented than on specimens examined from other areas. This gives the fish a much darker appearance than is usual.

Postmetamorphic coloration changes have been described as follows: At about 35 to 40 mm SL the dark belly spots are still distinct but are becoming overlaid by dermal pigmentation; at about 35 to 40 mm SL the spots along the lateral line begin to appear and the saddle-like marks on the back become darker (*12*: 14).

Experimentally induced changes in shade of color on different backgrounds have suggested that this fish apparently changes color shade by adaptation to external or environmental stimulus rather than by internal effect (*52*: 181). Other brief notes on changes in color are recorded (*8*: 52; *50*: 23).

Size. Most authors list the maximum size as 12 to 15 inches. Our largest specimen was 405 mm SL or slightly over 18 inches TL. Reports of specimens two feet long are unconfirmed (*71*: 139).

Habits. This fish has been described as a voracious feeder. A young aquarium specimen of about 35 mm SL was said to lunge at passing planktonic objects and, as its size increased, to take small fishes with equal vigor (*12*: 14). Feeding may be visually induced and probably occurs during the day (*32*: 290). Stomach contents of shrimp, crabs, squid, sea urchins, and annelids have been recorded, but fish are the principal food. The following types of fish have been reported as food: silversides (*Menidia*) (*45*: 353), menhaden (*Brevoortia*) (*2*: 88), *Anchoa mitchilli* (Valenciennes) and *Alutera schoepfii* (Walbaum) (*68*: 19), *Citharichthys macrops* Dresel (*17*: 67), *Pleuronectes americanus* Walbaum (*4*: 148), *Syacium gunteri* Ginsburg (*32*: 290), and *Cynoscion regalis* (Bloch and Schneider) (*35*: 131). Beebe and Tee-Van (*7*: 62) reported that a 35-mm *S. foetens* had eaten a 20-mm specimen of the same species, and that a 41-mm *S. foetens* had swallowed a 31-mm *S. foetens*.

Along the coast of the United States this lizardfish is found inshore in salt-water creeks, rivers, bays, sounds, and along the outer beaches, over both mud and sand bottoms; but it also ranges in the open ocean out over the continental shelf in depths to 100 fathoms. The young apparently prefer the inshore areas; those taken offshore are usually large specimens. Coles (*15*: 344) reported that they came into very shallow water at night and lay motionless under eelgrass or partially buried themselves in the sand. The depth record for the species is 100 fathoms—a 250-mm SL specimen from off northeastern Florida.

Apparently this species is seasonally migratory in the northern part of its range. Holbrook (*36*: 188) reported that *S. foetens* came into shallow water off the Carolina coast during June and remained into October but was found at all seasons in deep water along the coast. We have found no records of the species being taken north of North Carolina during the months of January through May. This migration may not apply to the Gulf coast of the United States, however, for Hildebrand (*32*: 290) stated that no seasonal trends were noted in its distribution in the bays and shallow Gulf waters of Texas. We have records from shallow Florida waters for all months except December. *S. foetens* has been recorded in a temperature range of 8.3 to 31.7° C (*68*: 19), and in a salinity range of 13.7 to 36.7 ‰ (*31*: 41); but it has been noted as most abundant in salinities above 25 ‰ and has been reported in Texas "landcuts" in salinities up to 60 ‰ (*70*: 182). Hildebrand (*33*: 201) suggested that this species seemed to be more common on mud bottoms off Texas and Tamaulipas than on a bottom of shell and calcareous sediment on Campeche Bank.

This species has been described as solitary in habitat (*15*: 345), but large numbers have been observed feeding voraciously on other small fish (*2*: 88). Thompson (*44*: 233) observed: "These fish, when resting on the bottom, lie with the head and shoulder girdle well elevated, then suddenly by a curious rocking and groveling motion settle down until only the top of the head is visible. When frightened they dart off a few yards, then settle down again by a repetition of this peculiar motion." Breder (*12*: 14, fig. 1) noted that a small aquarium specimen "would raise up with its body at an angle as it gave attention to some passing food object"; this he described as a "transitory pose," an extreme flexure in the vertical plane, the body bending sharply just back of the dorsal fin.

Young of *S. foetens* have been shown to be cannibalistic (*7*: 62). Predators recorded for *S. foetens* are barracuda (*10*: 13), *Paralichthys albigutta* Jordan and Gilbert (*68*: 19), and *Centropristis melanus* Ginsburg (*68*: 37). Copepods, acanthocephalids, nematodes, cestodes, and trematodes have been reported as parasites (*45*: 353; *46*: 86; *47*: 62, 120, 138; *51*: 375; *67*: 231; *72*: 260; *78*: 616, 626).

Relation to Man. The species is of no economic importance and apparently is seldom utilized as a foodfish. It is taken in numbers incidental to the shrimp fishery of the southern United States but is not marketed. Sport fishermen take it on occasion but generally consider it a nuisance. In the late nineteenth century, lizardfish were reported to have been handled cautiously when caught by South Carolina fishermen because of their supposed poisonous properties (*42*: 585).

Relationship to Extralimital Species. Based on descriptions given by Norman (*60*), Matsubara (*53*), and Schultz (*69*), and on our determinations, *Synodus foetens* is similar to the following nine Indo-Pacific species in having four or more rows of complete scales between lateral line and middle of dorsal-fin base: *S. altipinnis*, *S. scituliceps*, *S. lucioceps*, *S. lacertinus*, *S. variegatus*, *S. houlti*, *S. simulans*, *S. sechurae*, *S. ulae*, and *S. englemani*; the remaining Indo-Pacific species of *Synodus* have three such scale rows. *S. foetens* differs from *S. variegatus* and *S. houlti* in having a shorter head (20.6–26.3 °/₀ of SL in *S. foetens*; 27.5–30.8 °/₀ in *S. variegatus*; about 29.0 °/₀ in *S. houlti*). *S. foetens* differs further from *S. variegatus* in having a longer pelvic fin (15.8–21.3 °/₀ of SL in *S. foetens*; 11.1–14.0 °/₀ in *S. variegatus*) and in having a shorter dorsal base (10.6–12.5 °/₀ of SL in *S. foetens*; 15.1–17.3 °/₀ in *S. variegatus*). *S. foetens* differs from *S. lacertinus* in having the dorsal-fin origin nearer to the adipose fin than to the snout (dorsal origin nearer to snout in *S. lacertinus*), and in averaging a shorter head (20.6–26.3 °/₀ of SL in *S. foetens*; about 25–29.4 °/₀ in *S. lacertinus*). *S. foetens* differs from *S. simulans* in having the pectoral usually not extending to, or rarely extending slightly beyond, the pelvic origin (pectoral extending past pelvic- and dorsal-fin origins in the illustration of the type of *S. simulans*). *S. foetens* differs from *S. lucioceps* in averaging fewer lateral-line scales (56–65, usually 60–62, in *S. foetens*; 63–67 reported in *S. lucioceps*), and fewer rows of complete scales between the lateral line and the mid-dorsal-fin base (4–6 in *S. foetens*; about 7 reported for *S. lucioceps*); otherwise it is difficult to distinguish *S. foetens* from *S. lucioceps* on the basis of the published descriptions. *S. foetens* differs from *S. scituliceps* in the modal number of anal fin rays (11 in *S. foetens*; 13 in *S. scituliceps*), and in lacking a small fleshy knob at the tip of the lower jaw (present in *S. scituliceps*). *S. foetens* differs from *S. ulae* and *S. englemani* in having narrow pos-

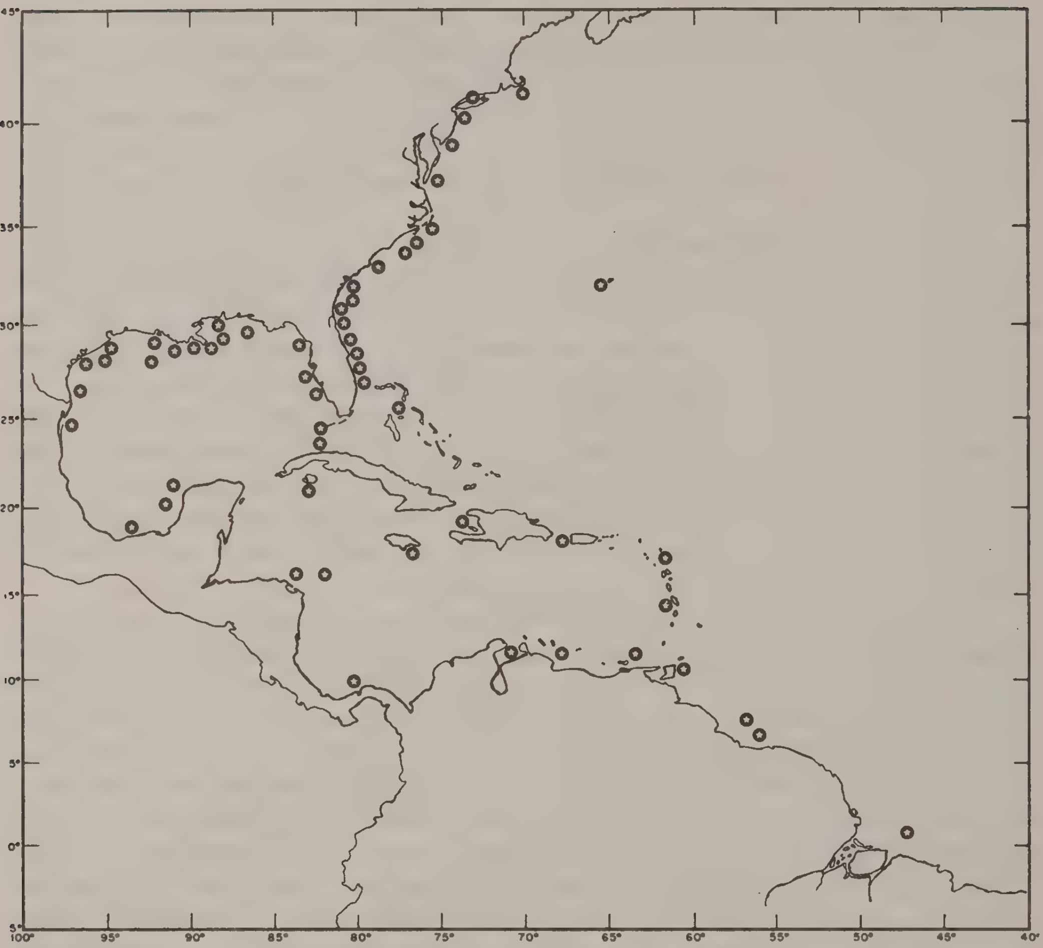

FIGURE 26. Distribution of *Synodus foetens* (circled stars). A record from Santa Catarina, Brazil, is not shown.

terior pelvic processes (broad in *S. ulae* and *S. englemani*), and in averaging a shorter pelvic fin (15.8–21.3 °/₀ of SL in *S. foetens*; 22.8–24.3 °/₀ in *S. ulae*; 21.3–23.2 °/₀ in *S. englemani*); *S. foetens* differs further from *S. ulae* in averaging fewer lateral-line scales (56–65 in *S. foetens*; 65–68 in *S. ulae*). *S. foetens* is difficult to distinguish from *S. altipinnis* on the basis of characters published for that species, but apparently *S. foetens* differs in having a shorter pectoral fin (38.0–53.7 °/₀ of head length in *S. foetens*; about 55.5 °/₀ in the holotype of *S. altipinnis*). *S. foetens* has not been distinguished from *S. sechurae*, but apparently the latter has the dorsal-fin origin more posteriorly placed and has a less-sharply pointed snout. *S. foetens* differs from *S. marchenae* in having more anal rays (8–9 in *S. marchenae*).

Synonymy. Fowler (25: 7, figs. 5, 6) described *Synodus bondi* from two specimens from Kingston, Jamaica, January 1935 (type, 275 mm, ANSP 68634; paratype, 194 mm, ANSP 68635). Comparison of the type and paratype with specimens of *Synodus foetens* removes all doubt that *S. bondi* is identical to *S. foetens*. We therefore include *S. bondi* in the synonymy of *S. foetens*. Contrary to counts given by Fowler, we found 60 lateral-line scales and 5 rows of complete scales above the lateral line in the paratype.

Range. Fig. 26. The species has a wide distribution along the Atlantic coast of the American continents, occurring from the vicinity of Cape Cod in the north to Brazil in the south. Within this broad area it occurs in some numbers from Long Island Sound, New York, to Cape Hatteras, North Carolina, and can be termed common along the coast of the United States from North Carolina to Florida. It is also common around the perimeter of the Gulf of Mexico. The species has been recorded from Bermuda, the Bahamas, Cuba, Puerto Rico, Haiti, Martinique, Jamaica, Trinidad, British Honduras, Panama, Venezuela, and Brazil.

Synonyms and References:

Salmo foetens Linnaeus, Syst. Nat., ed. 12, *1*, 1766: 513 (descr. based on Catesby, spec. from Dr. Garden of Charleston, S. Carolina, "Habitat in Carolina"; no type specimen indicated); Edwards *in* Catesby, Nat. Hist. Carolina, Florida, and Bahama Is., *2*, 1771: 1 (index page) (listed; Linnaeus' ident. of the Sea Sparrow-Hawk, *Saurus ex cinereo nigricans*, about 15 in. TL from Carolina coast); Bonnaterre, Tabl. Encyc. Meth. Reg. Nat., Ichthyol., 1788: 165, pl. 70, fig. 285 (descr.; Carolina); Gmelin, Linné Syst. Nat., *1* (3), 1789: 1385 (after Linnaeus 1766); Valenciennes *in* Cuvier and Valenciennes, Hist. Nat. Poiss., *22*, 1849: 462, 474, 477, 478 (discuss.); Jordan, Proc. U.S. nat. Mus., *7* (422), 1884: 191 (name *S. foetens* quoted).

Osmerus albidus Lacépède, Hist. Nat. Poiss., *5*, 1803: 229 (descr.), 235 (listed; based on Catesby and Linnaeus; type loc. Carolina; type spec. not designated).

Coregonus ruber Lacépède, Hist. Nat. Poiss., *5*, 1803: 243 (descr.), 263 (listed; based on Plumier; type loc. Martinique; type spec. not designated); Valenciennes *in* Cuvier and Valenciennes, Hist. Nat. Poiss., *22*, 1849: 473 (ref. to Lacépède 1803).

Salmo foeteus, Shaw, Gen. Zool., *5* (1), 1804: 67 (part; descr. based on Linnaeus 1766; excl. Bloch from synonymy).

Esox salmoneus Mitchill, Trans. lit. philos. Soc. N.Y., *1*, 1815: 442 (about 8 or 9 in. long; type loc. New York Bay; type spec. not designated).

Saurus longirostris Spix, Selecta Gen. Sp. Piscium, 1829: 80, pl. 43 (type loc. Brazil; described from 7- and 8.5-in. spec. in Museo Monacensi); 1831, pl. D (scales ill.); Valenciennes *in* Cuvier and Valenciennes, Hist. Nat. Poiss., *22*, 1849: 475 (ref., ill., descr. by Spix are exact); Castelnau, Exped. Cent. Amer. Sud, *3*, 1855 (Bahia, Brazil); Poey, Memorias Hist. nat. Cuba, *2* (2), 1860: 304 (diffs. between *S. longirostris* and *S. spixianus* Poey 1860); Poey, Repert. Fisico-Nat. Cuba, *1* (13–14), 1866: 382 (ref.); Poey, Repert. Fisico-Nat. Cuba, *2* (13–20), 1868: 414 (ref. close to *S. spixianus* Poey 1868); Poey, An. Soc. esp. Hist. Nat., *5* (1), 1876: 144 (ref. same as Poey 1866).

Saurus mexicanus Cuvier, Règne Anim., ed. 2, *2*, 1829: 314 (type loc. Gulf of Mexico; type spec. not designated); Griffith, Anim. Kingd., 1834: 430 (transl. from Cuvier 1829); Valenciennes, Poiss. *in* Règne Anim., ed. 3, *2*, 1837: 268 (copied after Cuvier 1829); Storer, Mem. Amer. Acad. Arts. Sci., *2*, 1846: 455 (diagn.; Mexico); Valenciennes *in* Cuvier and Valenciennes, Hist. Nat. Poiss., *22*, 1849: 476 (ref. corrects descr. by Cuvier 1829); Baird, 9th Ann. Rep. Smithson. Inst. (1854), 1855: 346 (Hudson River?, New York); Girard, Ichthyol. *in* U.S. Mex. Boundary Surv., *2* (2), 1858: 75 (coast of Texas); Holbrook, Ichthyol. S. Carolina, *1*, 1860: 191 (ref.).

Saurus conirostris, Cuvier, Règne Anim., ed. 2, *2*, 1829: 314 (ref. after Spix 1829; an apparent misprint for *Saurus longirostris*); Griffith, Anim. Kingd., 1834: 430 (transl. from Cuvier 1829); Valenciennes, Poiss. *in* Règne Anim., ed. 3, *2*, 1837: 268 (copied from Cuvier 1829).

Salmo foetans, Swainson, Nat. Hist. Fish. Amphib. Rept., *2*, 1838: 246 (systemat. posit.).

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Synodus synodus (Linnaeus) 1758

Lizardfish, Lagarto

Figures 11, 23, 27, 28

Study Material. A total of 49 specimens ranging in length between 33 and 150 mm, from: Bahamas. One specimen, 113 mm, N. shore of Rose I., March 25, 1955, ANSP 74937; 1, 140 mm, N. shore of New Providence I., April 16, 1955, ANSP 74940; 4, 33–74 mm, sw. end of Silver Cay, July 24, 1955, ANSP 74941; 3, 38–94 mm, S. shore of Salt Cay, Aug. 27, 1955, ANSP 74951; 2, 54 and 93 mm, N. shore of New Providence I., Sept. 5, 1955, ANSP 74952; 13, 36–116 mm, near Lyford Cay, New Providence I., May 8, 1956, ANSP 74956.

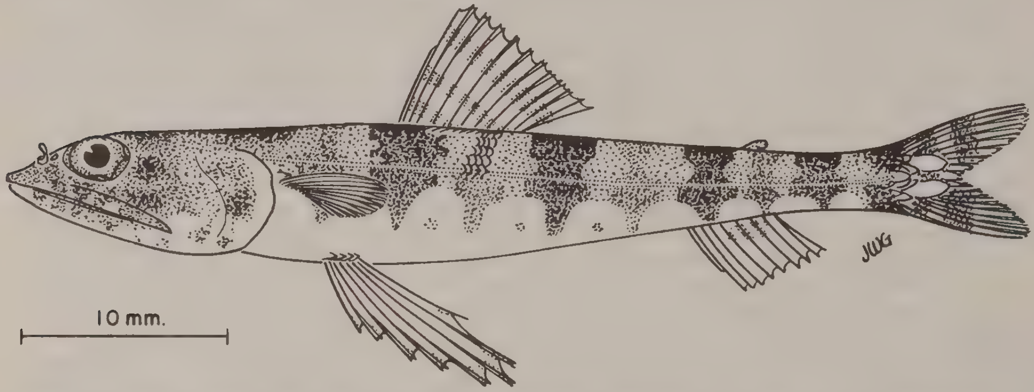

Figure 27. *Synodus synodus*, 43.0 mm SL, Ocho Rios, Jamaica, Caldwell St. C-6-2257-IJ, UF (uncatalogued).

Gulf of Mexico. Fourteen specimens, 42–94 mm, Oregon, Campeche Bank (Arcas Cay), Dec. 6–7, 1952, CNHM 45391; 3, 137–150 mm, Silver Bay St. 775, 27°42′N, 84°11′W, 30 fms., Sept. 12, 1958, BLBG; 1, 35 mm, $^{1}/_{4}$ mi. SW. of Alligator Reef, Monroe Co., Florida, 20 ft., May 10, 1958, UMML 3502; 1, 104 mm, 8 mi. NE. of Alligator Reef, Florida, 40 ft., Sept. 28, 1958, UMML 4895.

Caribbean. Two specimens, both 43 mm, Ocho Rios, Jamaica, June 22, 1957, UF; 3, 68–81 mm, Oregon St. 1892, 15°30′N, 81°04′W, 16 fms., Aug. 24, 1957, BLBG; 1, 87 mm, Oregon St. 2054, 04°02′N, 50°20′W, 50 fms., Nov. 14, 1957, BLBG.

Distinctive Characters. See *Key to Atlantic Species*, p. 48.

Description. Proportional dimensions in per cent of standard length, with ranges given first, followed by the mean in parentheses, based on measurements from 11 specimens: 36, 43, 51, 68, 76, 81, 94, 113, 116, 140, and 150 mm SL.

Body at base of pelvic fin: depth 11.6–16.1 (14.4); width 11.2–17.1 (14.3).

Head: length 27.2–30.6 (28.9).

Snout: length 5.5–7.9 (6.4).

Eye: diameter 4.6–7.4 (6.0).

Interorbital: width 1.8–3.2 (2.5).

Premaxillary: length 15.0–19.1 (17.9).

Distance from snout to origin of: dorsal fin 40.7–44.4 (42.3); anal fin 75.8–81.4 (79.2); pelvic fin 33.6–38.0 (35.5).

Distance from: origin of dorsal fin to origin of adipose fin 38.0–42.3 (40.0); tip of pectoral fin to origin of pelvic fin +3.2 to +6.6 (+4.8).

Dorsal fin: length of base 14.5–16.4 (15.5); length of longest ray 13.4–16.3 (15.0); length of last ray 7.5–9.1 (8.4).

Anal fin: length of base 8.7–10.3 (9.2).

Pectoral fin: length of longest ray 9.8–13.5 (11.3).

Pelvic fin: length of first ray 8.0–11.1 (9.0); length of longest ray 20.0–27.2 (24.8).

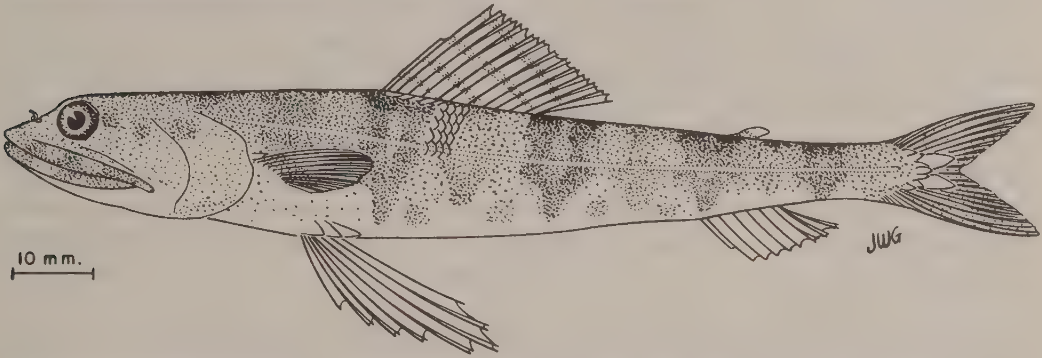

FIGURE 28. *Synodus synodus*, 113 mm SL, north shore of Rose Island, Bahamas, St. 198, ANSP 74937.

Counts, based on 47 specimens.

Scales: predorsal 15–18 (7 specimens with 15, 21 with 16, 13 with 17, 1 with 18); rows of complete scales between lateral line and base of dorsal fin 4 (all specimens), 5 reported.[14]

Lateral-line scales: 54–59 (1 with 54, 10 with 55, 20 with 56, 14 with 57, 1 with 58, 1 with 59), up to 60[15] and 62[16] reported.

Fin rays: dorsal fin 12–14 (22 with 12, 24 with 13, 1 with 14), 11 (rarely)–15 reported;[17] anal fin 8–10 (11 with 8, 31 with 9, 5 with 10), 11 reported (*55*: 11); pectoral fin 11–12 (5 with 11, 42 with 12), 13 reported (*60*: 109).

HEAD but slightly compressed; top of head very rugose. SCALES small. LATERAL LINE not well marked; no keel on caudal peduncle. SNOUT rounded, blunt, its length greater than eye diameter on specimens over about 50 mm SL. INTERORBITAL space moderately concave. LOWER JAW included or subequal to upper jaw, not ending in a fleshy knob. DORSAL fin with anterior rays not extending to, or beyond, tips of any of succeeding rays when laid back; its origin closer to adipose fin than to tip of snout.

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[14] Norman (*60*: 112) gave a count of 4.5 to 5.5 scales for the synonymous *S. meleagrides*. Clark (*14*: 49) reported 5.

[15] Norman (*60*: 112) gave a count of 58 to 60 lateral-line scales for *S. meleagrides*.

[16] Clark (*14*: 49) reported 60 to 62 scales in "longitudinal series."

[17] Norman (*60*: 109, 112) reported 11 rarely for *S. synodus* and 15 for *S. meleagrides*. Clark (*14*: 49) and Maul (*55*: 11) recorded 14 to 15 for *S. synodus* from St. Helena and Madeira.

Anal base much shorter than dorsal base, its length 53.0–65.8 % of dorsal-base length. Pectoral fin with tip extending beyond origin of pelvic fin. Pelvic fin with 6th ray the longest. Pelvic bones with posterior processes long, flat and broad with acute tip and a mid-dorsal ridge diminishing distally. Vertebrae 52 or 53.[18]

Color. One of the most distinctively marked of our species (Fig. 28). In preservative, background on head, back, and sides light grey. Small dark spot near tip of snout; blotches on sides of jaws; a more or less dark patch on shoulder girdle. Four broad brown saddles extending down sides to well below lateral line; the 1st at origin of dorsal fin, the 2nd just posterior to dorsal fin, the 3rd just anterior to adipose fin, and the 4th about midway between adipose fin and base of caudal; less distinct brownish blotches between the saddles, some crossing the back in an interrupted pattern; a broad dark band at nape of neck extending down the sides to insertion of pectoral fins. Belly and lower sides white. Dorsal fin with barred pattern; caudal light dusky; pectoral, pelvic, and anal fins pale; adipose dusky at base and pale at tip. Young specimens with similar basic coloration and pattern, but with saddles and intermediate blotches much brighter in color (Fig. 27).

C. Richard Robins of The Marine Laboratory, University of Miami, kindly furnished color notes of a 104-mm SL specimen (UMML 4895) from eight miles northeast of Alligator Reef, Monroe County, Florida, taken September 28, 1958:

> The body . . . when freshly preserved was banded with red and orange-grey markings (four red markings distinct on body). Grey patches on the head and body broken by symmetric orange-red and red markings; eyes, red-orange. Underside pale except for the anterior part of the pelvic fins where the background color is broken by lines of red dots. All fins are dusky banded with red.

Size. The largest specimen examined from the western North Atlantic, taken in the eastern Gulf of Mexico, was 150 mm SL. Norman (*60*: 110, 112) reported specimens of 290 mm TL from Madeira and of 330 mm TL from St. Helena, the latter under the name of *S. meleagrides.*

Habits. This species apparently is primarily an inhabitant of inshore areas, as the majority of specimens taken, both in the eastern and western Atlantic, have been from such a habitat. The fact that seven specimens were taken by the vessels Oregon and Silver Bay (3 at 30 fathoms in the eastern Gulf of Mexico, 3 at 16 fathoms in the western Caribbean, and 1 at 50 fathoms off northern Brazil) indicates that the species does venture into open areas over the continental shelf.

Essentially nothing has been recorded on the behavior, food, or enemies of this species.

Relation to Man. The species is of little or no significance to man. Melliss (*56*: 110) reported this species in St. Helena as "good as food, but not very abundant—too bony to be popular, excepting with the labouring people."

Relationship to Extralimital Species. Based on key characters and descriptions by Norman (*60*), Matsubara (*53*), and Schultz (*69*), and on our determinations, *S. synodus,* with a range of 8 to 11 anal rays, is either similar to, or overlaps, in this character, the species mentioned below. *S. synodus* differs from *S. hoshinonis*, *S. indicus*, *S. kaianus*, *S. fuscus*, *S. macrops*, and *S. binotatus* in having 4 or 5, rather than 3, rows of complete scales above the lateral line. *S. synodus* differs from *S. ulae* and *S. englemani* in having fewer lateral-line scales and fewer predorsal scales (54–62 and 15–18, respectively, in *S. synodus*; 65–68 and 19–20 in *S. ulae*; 62–64 and 19 in *S. englemani*). *S. synodus* has a shorter anal base than dorsal base in direct contrast to *S. scituliceps* (anal base 53–65.8 % of dorsal base in *S. synodus*; about 125 % in *S. scituliceps*). *S. synodus* apparently differs from *S. variegatus*, *S. lacertinus*, *S. sechurae*, *S. houlti*, and *S. simulans* in having a small dark spot near the tip of the snout, this being absent in the other four species. *S. synodus* loses its larval characters at a smaller size than does *S. marchenae*, the latter possessing larval characters at 46–51 mm SL.

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[18] Arambourg (*1*: 39) recorded 35+17 or 18.

Synonymy. *Synodus meleagrides* (Valenciennes) has been reported only from the coasts of Uruguay and St. Helena, and Norman (*60*: 111, fig. 7), though treating it as a distinct species, suggested that it might be synonymous with *S. synodus*. Comparison of the descriptive characters reported by Norman (based on three types in the Paris Museum and five specimens in the British Museum) with data from a series of *S. synodus* from the Bahamas shows that the vertical fin-ray counts and lateral-line scale counts, though higher in *S. meleagrides*, overlap to such an extent in the two forms that the differences are not sufficient for species separation. Snout length against eye diameter is too variable to be a reliable distinctive character. We therefore include *S. meleagrides* in the synonymy of *S. synodus*.

Range. Fig. 23. This species occurs on both sides of the Atlantic. In the western Atlantic its range apparently extends from the Gulf of Mexico and the West Indies to Uruguay. Within this area records exist from off Tampa, Florida, Campeche Bank in the southern Gulf of Mexico, various localities in the Bahamas, in Jamaica, Bonaire and St. Eustatius in the Dutch West Indies, the western Caribbean, Bay of Santa Marta in Colombia, off northern Brazil, Bahia in Brazil, and Montevideo, Uruguay. In the eastern Atlantic it has been taken at Madeira and the Canary Islands.

Synonyms and References:

Esox synodus Linnaeus, Syst. Nat., ed. 10, *1*, 1758: 313 (descr. based on *Synodus* of Gronow, Mus. Ichthyol., *1* [151], 1754: pl. 7, fig. 1; *fide* Norman, Proc. zool. Soc., London, 1935: 109; type loc. "Habitat in America"; no type spec. known); Linnaeus, Syst. Nat., ed. 12, *1*, 1766: 516 (descr. based on Gronow 1754); Bonnaterre, Tabl. Encyc. Meth. Ichthyol., 1788: 174, pl. 72, fig. 295 (descr.; America); Gmelin, Syst. Nat., *1* (3), 1789: 1390 (after Linnaeus 1766); Bloch, Ichthyol. Hist. Nat. Poiss., *2*, 1796: 335 (ref.); Shaw, Genl. Zool., *5* (1), 1804: 108 (after Linnaeus 1766); Cuvier, Règne Anim., *1*, 1817: 169 (ftn. 2 ref. after Gronow 1763); Cuvier, Règne Anim., ed. 2, *2*, 1829: 314 (ref.); Griffith, Anim. Kingd., *10*, 1834: 430 (ref.; *synodus* of Gronow of doubtful ident.); Valenciennes, Poiss. *in* Règne Anim., ed. 3, *2*, 1837: 268 (ref.); Valenciennes *in* Cuvier and Valenciennes, Hist. Nat. Poiss., *22*, 1849: 462 (discuss.); Jordan, Proc. U.S. nat. Mus., *9* (593), 1887: 526 (ref.; specimen in Paris. Mus. perhaps Linnaeus type); Fowler, Proc. Acad. nat. Sci. Philad., *77*, 1925: 200 (ref.; E. Africa, as *Synodus synodus*); Norman, Proc. zool. Soc. London, 1935: 111 (ref.); Whitley, Aust. Zool., *8* (4), 1937: 119 (as type species of *Synodus*).

Synodus synodus, Meuschen, Mus. Gronovium, 1778: 35 (name of Gronow's no. 351, 1763; *fide* Norman, Proc. zool. Soc. London, 1935: 109, and Whitley, Rec. Aust. Mus., *17*, 1929: 304); Meuschen, Index Cont.

Nom. Gen. Spec. Prop. Triv. Syn., 1781 (index name of Gronow's *Synodus*, 1763; *fide* Whitley 1929: 304); Bloch and Schneider, Syst. Ichthyol., 1801: 396 (descr. after Gronow 1754, Linnaeus 1758, and Gmelin 1789); Cuvier, Règne Anim., *1*, 1817: 169 (ftn. 2, discuss.); Cuvier, Règne Anim., ed. 2, *2*, 1829: 314 (same as Cuvier 1817); Valenciennes, Poiss. *in* Règne Anim., ed. 3, *2*, 1837: 268 (ftn. 2, discuss.); Jordan, Proc. U.S. nat. Mus., *9* (593), 1887: 526 (spec. of Cuvier and Valenciennes, Hist. Nat. Poiss., *22*, 1849, from Bahia, Brazil, in Paris Mus., exam. and descr.); Jordan, Proc. U.S. nat. Mus., *9* (595), 1887: 563 (part; excl. "*Saurus intermedius* Spix" from synonymy); Jordan and Evermann, Rep. U.S. Comm. Fish and Fish. (1895), *21* (5), 1896: 296 (Bahia, Brazil); Jordan and Evermann, Bull. U.S. nat. Mus., *47* (1), 1896: 536 (descr.; key; synonymy in part, excl. *Saurus varius* by Günther 1864, which is *S. variegatus*; Bahia, Brazil); Evermann and Marsh, Bull. U.S. Fish Comm. (1900), *20* (1), 1902: 92 (key); Jordan and Herre, Proc. U.S. nat. Mus., *32* (1544), 1907: 518 (ref.; discuss.); Clark, Proc. roy. Soc. Edinb., *19* (9), 1914: 49, figs. 2–4 (descr.; St. Helena); Tåning, Rep. Danish oceanogr. Exped. [1908–10] Medit., *5*, 1918: 4 (ref. to Regan, Brit. Mus. nat. Hist., Zool., *1* (4), 1916), 149 (postlarvae; W. Indies); Nichols, Bull. Amer. Mus. nat. Hist., *44* (3), 1921: 22 (Turks I., Bahamas); Arambourg, Matér. géol. Algér., (1) *6*, 1927: 37 (descr.; *cf.* fossil *Synodus avus*); Borodin, Bull. Vanderbilt Oceanogr. (Mar.) Mus., *1* (1), 1928: 9, 10 (Jamaica and Caribbean); Whitley, Rec. Aust. Mus., *17*, 1929: 304 (ref. to ident. of names of Gronow 1763 by Meuchen 1781); D'Erasmo, Atti Accad. Sci. fis. mat. Napoli, (2) *18*, 1930: 38 (ref.); Jordan, Evermann, and Clark, Rep. U.S. Comm. Fish. (1928), App. 10, 1930: 163 (in check list); Norman, Proc. zool. Soc. London, 1935: 100, fig. 1 B (young ill.); 103 (key); 109, fig. 5 (synonymy; descr.; Madeira; s. W. Indies; Bay of Santa Marta, Colombia; Bonaire and St. Eustatius, Dutch W. Indies; Bahia, Brazil), 111, fig. 6 B (*cf. S. variegatus*); Fowler, Bull. Amer. Mus. nat. Hist., *70* (1), 1936: 344 (based on Clark 1914); Fowler, Bull. Amer. Mus. nat. Hist., *70* (2), 1936: 1219 (W. Africa); Whitley, Aust. Zool., *8* (4), 1937: 219 (ref. to proposed subgenus *Synodus*); Matsubara, J. Imp. Fish. Inst. Tokyo, *33* (1), 1938: 8 (brief *cf. S. variegatus*); Fowler, Arqu. Zool. Estad. São Paulo, *3* (6), 1941: 140 (Brazil); Fowler, Monogr. Acad. nat. Sci. Philad., *6*, 1944: 438, 459 (Turks I. and Santa Marta Bay, Colombia); Maul, Bol. Mus. Municipal Funchal, *2* (2), 1946: 11, fig. 2 (descr.); Hildebrand, Smithson. misc. Coll., *110* (9), 1948: 12 (*cf. S. cinereus*); Maul *in* Noronha and Sarmento, Vertebr. Madeira, Peixes, ed. 2, 1948: 142 (Madeira); Cadenat, Inst. Franc. Afr. noire, *3*, 1950: 153, fig. 52 (Senegal, W. Africa); Fowler, Caldasia, *6* (27), 1953: 51 (Caribbean Colombia); Smith, Sea Fish. S. Africa, rev. ed., 1953: 112 (descr.; questions Natal, SE. Africa, record); Springer and Bullis, U.S. Fish. Wildl. Serv., Sp. Sci. Rep. Fish. 196, 1956: 54 (OREGON at Arcas, Campeche Bank); Briggs, Bull. Fla. State Mus., Biol. Sci., *2* (8), 1958: 257 (range, in part; excl. ref. to Tortugas, Florida, based on Longley and Hildebrand, Publ. Carnegie Inst. Wash., *34* (535), 1941: 22); Gibbs, Copeia, 1959: 235, fig. 1 E (larvae descr.).

Synodus fasciatus Lacépède, Hist. Nat. Poiss., *5*, 1803: 319 (descr.), 321 (based on Linnaeus; habitat given as Mediterranean).

Saurus meleagrides Valenciennes in d'Orbigny, Voy. Amer. Merid., Poiss., 1847: 10, pl. 11, fig. 3, plate publ. in 1834 (*fide* Norman, Proc. zool. Soc. London, 1935: 111, type loc. Montevideo, Uruguay, type spec. 200–250 mm, MNHN 3416; *fide* Bertin and Estève, Impremeria Nat., *6*, 1950: 7); Clark, Proc. roy. Phys. Soc. Edinb., *19* (9), 1914: 50 (ref.; *cf. S. synodus*); Bertin and Estève, Bull. Mus. Hist. nat. Paris, 1952: 7 (3 syntypes reported in Paris Mus. from Montevideo, Uruguay).

Saurus synodus, Valenciennes *in* Cuvier and Valenciennes, Hist. Nat. Poiss., *22*, 1849: 477 (part; descr.; Martinique and Guadeloupe, Lesser Antilles; Bahia, Brazil; St. Helena; excl. records from Indo-Pacific, which probably refer to *S. variegatus*); Poey, Repert. Fisico-Nat. Cuba, *1* (13–14), 1866: 382 (Cuba); Jordan, Proc. U.S. nat. Mus., *9* (593), 1887: 525 (ref. to Cuvier and Valenciennes 1849, Bahia spec.); Norman, Proc. zool. Soc. London, 1935: 110 (exam. spec. rep. Metzelaar, Rapp. Bet. Voor. Ind. Zee. Kol., Curacao, *2* (2), 1919, and by Valenciennes *in* Cuvier and Valenciennes 1849).

Saurus meleagris, Valenciennes *in* Cuvier and Valenciennes, Hist. Nat. Poiss., *22*, 1849: 484 (descr.; Buenos Aires, Argentina; after *Saurus meleagrides* Valenciennes, from Montevideo, Uruguay); Devincenzi, An. Mus. Hist. nat. Montevideo, *2* (6), 1924: 99 (Montevideo, after Cuvier and Valenciennes 1849).

Saurus atlanticus Johnson, Proc. zool. Soc. London, 1863: 41 (type loc. Madeira; holotype in British Mus. [Nat. Hist.], 290 mm TL; *fide* Norman, Proc. zool. Soc. London, 1935: 110); Günther, Cat. Fish. British Mus., *5*, 1864: 395 (descr.; Madeira); Steindachner, S.B. Akad. Wiss. Wien, *57* (1), 1868: 768 (Santa Cruz de Tenerife market, Canary Is.); Günther, Proc. zool. Soc. London, 1869: 238 (St. Helena); Melliss, St. Helena Pisces, 1875: 110 (St. Helena); Günther, Rep. Deep-Sea Fish. Voy. 'Challenger', *22*, 1887: 179 (probably descends to moderate depths); Jordan, Proc. U.S. nat. Mus., *9* (593), 1887: 526 (discuss.); Sauvage, Hist. Nat. Poiss., Madagascar, *16*, 1891: 526 (Madagascar); Vinciguerra, Atti Soc. Ital. Sci. nat. (1892), *34*, 1893: 329 (Canary Is.); Metzelaar, Rapp. Bet. Voor. Ind. Zee. Kol. Curaçao, *2* (2), 1919: 214 (trop. W. Africa); Fowler, Proc. Acad. nat. Sci. Philad., *77*, 1925: 200 (discuss.).

Synodus atlanticus, Goode and Bean, Sp. Bull. U.S. nat. Mus., *2*, 1895: 57 (discuss.); Arambourg, Matér. géol. Algér., (1) *6*, 1927: 39 (*cf.* fossil *Synodus avus*); D'Erasmo, Atti Accad. Sci. fis. mat. Napoli, (2) *18*, 1930: 38 (ref.); Norman, Proc. zool. Soc. London, 1935: 110 (exam. holotype).

Saurus varius (*non* Lacépède), Voltz, Natuurk. Tijdschr. Ned.-Ind., *66*, 1907: 175 (part; ref. to Brazil and México after *Synodus synodus* ref. of Bleeker; excl. other ref., which is to *S. variegatus* from Indo-Pacific).

Saurus (*Synodus*) *synodus*, Metzelaar, Rapp. Bet. Voor. Ind. Zee. Kol. Curaçao, *2* (2), 1919: 22 (descr.; Bonaire and St. Eustatius, Dutch W. Indies).

Saurida gracilis (*non* Quoy and Gaimard), Metzelaar, Rapp. Bet. Voor. Ind. Zee. Kol. Curaçao, *2* (2), 1919: 23 (descr.; St. Eustatius, Dutch W. Indies; *fide* Norman's 1935 exam. of spec.); Norman, Proc. zool. Soc. London, 1935: 110 (reident. of spec. rep. by Metzelaar).

Synodus nicholsi Breder, Bull. Bingham oceanogr. Coll., *1* (1), 1927: 13, fig. 6 (type loc. Royal I., Eleuthera, Bahamas; type BOC 56, 99 mm TL); Norman, Proc. zool. Soc. London, 1935: 110 (synon. with *S. synodus*); Fowler, Monogr. Acad. nat. Sci. Philad., *6*, 1944: 438 (after Breder 1927); Hildebrand, Smithson. misc. Coll., *110* (9), 1948: 13 (*cf. S. cinereus*).

Saurida nebulosa (*non* Valenciennes), Jordan, Evermann, and Clark, Rep. U.S. Comm. Fish. (1928), App. 10, 1930: 164 (W. Indies N. to St. Eustatius; apparently based on erroneous ident. of *Saurida gracilis* by Metzelaar 1919).

Synodus synodus atlanticus, Norman, Proc. zool. Soc. London, 1935: 111 (speculation on relationships).

Synodus meleagrides, Norman, Proc. zool. Soc. London, 1935: 103, 111, fig. 7 (key; descr.; St. Helena; Montevideo, Uruguay; a possible synonym of *S. synodus*); Fowler, Bull. Amer. Mus. nat. Hist., *70* (2), 1936: 1219 (based on Norman 1935); Whitley, Aust. Zool., *8* (4), 1937: 219 (incl. in proposed subgenus *Synodus*); Bertin and Estève, Impremeria Nat., *6*, 1950: 7 (ref. to type spec.); Gibbs, Copeia, 1959: 232 (ref.).

Probable Reference:

Synodus (species not given), Lowe, Proc. zool. Soc. London, *11*, 1843: 89 (described black spot on tip of snout suggests this ident.; Madeira).

Questionable Reference:

Synodus synodus, Regan, Rep. Brit. Antarctic Exped., Zool., *1* (4), 1916: 135 (S. Atl.), pl. 7, fig. 4 (ill. larva); 137 (14-mm larva descr.; 20°30′ S, 36°30′ W, off Brazil; may have been *Synodus saurus*); 150 (ref. to p. 137, pl. 7, fig. 4).

Negative References:

Not *Saurus synodus* (Linnaeus), Bleeker, Natuurk. Tijdschr. Ned.-Ind., *2*, 1851: 228, 257 (descr.; excl. most of synonymy; ref. is to *Synodus variegatus* from Bandanaira, Moluccas); Bleeker, Verh. Batavia Genoot., *24*, 1852: 3, 6, 28 (ref. is to *S. variegatus* from the Sunda and Moluccas Is.); Bleeker, Natuurk. Tijdschr. Ned.-Ind., *3*, 1852: 234, 250 (ref. is to *S. variegatus* from Banda, Moluccas); Bleeker, Natuurk. Tijdschr. Ned.-Ind., *12*, 1856–1857: 231, 235 (ref. is to *S. variegatus* from Batu Is., Indonesia); Bleeker, Natuurk. Tijdschr., Ned.-Ind., *13*, 1857: 374 (ref. is to *S. variegatus* from Sangi Is., Indonesia); Bleeker, Natuurk. Tijdschr. Ned.-Ind., *15*, 1858: 60 (ref. is to *S. variegatus* from Java); Bleeker, Natuurk. Tijdschr. Ned.-Ind., *15*, 1858: 201 (ref. is to *S. variegatus* from Goram Is., Moluccas); Bleeker, Natuurk. Tijdschr. Ned.-Ind., *15*, 1858: 461 (ref. is to *S. variegatus* from Kokos I.); Bleeker, Natuurk. Tijdschr. Ned.-Ind., *17*, 1858–1859: 143, 151 (ref. is to *S. variegatus* from Bali, Indonesia); Bleeker, Acta Soc. Sci. Indo-Neerl., *8*, 1860: 50 (ref. is to *S. variegatus*; *fide* Weber and de Beaufort, Fish. Indo-Austr. Archipel., *1*, 1911: 344); Bleeker, Acta Soc. Sci. Indo-Neerl., *8*, 1860: 56 (ref. is to *S. variegatus*; *fide* Weber and de Beaufort, 1911: 344); Bleeker, Versl. Akad. Amst., *12*, 1861: 32, 62 (ref. is to *S. variegatus* from Singapore); Bleeker, Versl. Akad. Amst., *12*, 1862: 112 (ref. is to *S. variegatus* from Bachan I., Moluccas); Jouan, Mem. Soc. Imp. Sci. Nat. Cherbourg, *13*, 1867: 271 (ref. to *S. variegatus* from Hong Kong).

Not *Synodus synodus* (Linnaeus), Bleeker, Ned. Tijdschr. Dierk., Amst., *1*, 1863: 156 (ref. is to *Synodus variegatus* from Halmahera I., Moluccas); Bleeker, Ned. Tijdschr. Dierk., Amst., *1*, 1863: 237 (ref. is to *S. variegatus* from Ternate I., Moluccas); Bleeker, Ned. Tijdschr. Dierk. Amst., *2*, 1865: 193 (ref. is to *S. variegatus* from Wahai, and Ceram I., Moluccas), 291 (ref. is to *S. variegatus* from Amboina I., Moluccas); Jouan, Mem. Soc. imp. Sci. Nat. Cherbourg, *13*, 1868: 271 (ref. is to *S. variegatus* = *S. japonicus*, from Hong Kong; *fide* Fowler, Hong Kong Nat., 3 (3–4), 1932: 256); Bleeker, Versl. Akad. Amst., *2* (7), 1873: 36 (listed), 39 (Aru Is., Moluccas); Bleeker, Atlas Ichthyol., *6*, 1875: 145, pl. II, fig. 5 (ref. is to *S. variegatus*; *fide* Norman, Proc. zool. Soc. London, 1935: 106); Bleeker, Arch. Neerl. Sci. Nat., *13*, 1878: 55 (ref. is to *S. variegatus* from New Guinea); Bleeker, Verh. Akad. Amst., *18*, 1879: 24 (ref. is to *S. variegatus* from Japan); Weber, Senckenbergiana, *34*, 1911: 4 (ref. is to *S. variegatus* from Aru Is., Moluccas); Weber, Fische 'Siboga'-Exped., 1913: 81, fig. 28 (ref. is to larval *S. variegatus* from Indonesia); Fowler, Proc. Acad. nat. Sci. Philad., *77*, 1925: 200 (descr.; Natal, S. Africa; following Norman, Proc. zool. Soc. London, 1935: 111, on separation of the similar *S. synodus* and *S. variegatus*, this 275-mm TL spec. was *S. variegatus*); Barnard, Ann. S. Afr. Mus., *21* (2), 1927: 1020 (ref. to record of Fowler 1925); Longley and Hildebrand, Publ. Carnegie Inst. Wash., *34* (535), 1941: 22 (descr.; not *S. synodus* because of the higher number of anal rays, 11; not *S. saurus* because of high number of scales between lateral line and dorsal base, 5; probably *S. foetens* for the above and other reasons; Tortugas, Florida).

Not *Saurus synodon*, Bleeker, Verh. Batavia Genoot., *24*, 1852: 5 (ref. is to *Synodus variegatus* from the Sunda and Moluccas Is.).

Not *Saurus atlanticus* Johnson, Playfair and Günther, Fish. Zanzibar, 1866: 115 (ref. is to *Synodus indicus* from Zanzibar; *fide* Norman's exam. of spec. in Brit. Mus., Proc. zool. Soc. London, 1935: 114).

Genus *Saurida* Valenciennes 1849

Lizardfish

Saurida Valenciennes *in* Cuvier and Valenciennes, Hist. Nat. Poiss., *22*, 1849: 499; type species *Salmo tumbil* Bloch 1795, by subsequent designation of Jordan, Tanaka, and Snyder, J. Coll. Sci. Tokyo, *33* (1), 1913: 53, *fide* Fowler, Bull. Amer. Mus. nat. Hist., *70* (2), 1936: 1218.

Characters. Body elongate and almost cylindrical, the depth at origin of pelvic fins slightly greater than, or about equal to, width. Head depressed; bone surfaces on top of head little if at all rugose. Nostrils placed from well forward to about midway on the snout. Eye with wide to narrow adipose eyelid on anterior and posterior margins. Interorbital space almost flat. Snout blunt, its length longer or shorter than eye. Lower jaw longer or shorter than upper jaw; no fleshy knob at tip. Teeth in bands in both jaws (the inner teeth the largest), slender, pointed, depressible, some arrow-shaped at the tips and visible when mouth is closed; similar teeth on the palate, in two bands on each palatine, with the inner band shorter than the outer band; head of vomer sometimes with small teeth; similar teeth on tongue and branchial arches. Vomer present. Branchiostegals 13–16. Scales moderate to large; pectoral axillary scale moderate to very long and pointed; modified scales extending in a single median series onto midcaudal rays. Lateral line well marked, especially on caudal peduncle. Anal fin short, its origin much nearer to base of caudal than to head; its base usually shorter than, but sometimes nearly equal to, dorsal base; first 2 rays unbranched, other rays branched. Dorsal fin with anterior rays extending beyond the tips of all succeeding rays when laid back. Pectorals with tips extending to or much beyond pelvic origins and either not reaching or extending past dorsal origin. PELVIC rays 9, the median rays usually longer than outer rays. Pelvic bones with posterior processes flat and broad, slightly expanded in distal portion with acute to blunt tip, and a low dorsal ridge on lateral margin of proximal portion (*S. normani* Longley, *S. caribbaea* Breder, *S. brasiliensis* Norman, and *S. suspicio* Breder).

Habits. Nothing has been reported on the food, behavior, or breeding habits of the Atlantic species of *Saurida*. Three of the Atlantic species apparently exist in an offshore bottom habitat at depths of generally less than 100 fathoms but extending down to 300 fathoms. The relatively rare *S. suspicio* may utilize a more littoral habitat. Some Indo-Pacific species occur at shallower depths and have been reported to abound in coral sand on reefs (*38*: 433) and to frequent muddy bottom along coasts (*63*: 62).

Relation to Man. The generally deep-water habitat and suggested numerical scarcity of the Atlantic species of *Saurida* preclude their being of direct importance to man. However, Indo-Pacific forms of greater numerical abundance have been used as food.[19]

Numerical Abundance. Available records indicate the order of comparative abundance of the western Atlantic species from most to least abundant as: *S. brasiliensis*, *S. normani*, *S. caribbaea*, and *S. suspicio*. However, these species apparently comprise a very small portion of the fish fauna. Only 12 specimens of *S. suspicio* have been recorded.

Species. Nine species of *Saurida* are known from various parts of the world. Five of these are Indo-Pacific,[20] but one has been reported from the Mediterranean Sea.[21] *Saurida* is not known from the west coast of the American continents. Four species are known only from the Atlantic Ocean, with one of these occurring in the eastern and western Atlantic and the other three known only from the western North Atlantic.

Key to Atlantic Species

1a. Lower jaw shorter than upper jaw, not visible from above when mouth is closed. *normani* Longley 1935, p. 86.

1b. Lower jaw longer than upper jaw, distinctly visible from above when mouth is closed.

  2a. Scales in lateral line 40–50. *brasiliensis* Norman 1935, p. 90.

  2b. Scales in lateral line 51–60.

    3a. Three rows of complete scales between lateral line and base of dorsal fin; pectoral fin with tip reaching about to, or barely past, origin of pelvic fin, its length 10.9–12.8 % of SL. *suspicio* Breder 1927, p. 94.

    3b. Four rows of complete scales between lateral line and base of dorsal fin; pectoral fin with tip reaching much beyond origin of pelvic fin, its length 17.5–20.0 % of SL. *caribbaea* Breder 1927, p. 97.

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[19] Jenkins (*38*: 433) reported *Saurida gracilis* Quoy and Gaimard sold in the market at Hawaii. Okada (*63*: 62) reported *S. undosquamis* (Richardson) to be eaten fresh and as fish-cake in Japan.

[20] *Saurida tumbil* (Bloch) 1795, *S. gracilis* (Quoy and Gaimard) 1824, *S. elongata* (Temminck and Schlegel) 1846, *S. undosquamis* (Richardson) 1848, *S. longimanus* Norman 1939.

[21] Ben-Tuvia (*9*: 7, fig. 2) reported *S. grandisquamis* [= *S. undosquamis* (Richardson)] from off Israel.

Saurida normani Longley 1935

Figures 29, 30

Study Material. A total of 39 specimens ranging in length between 75 and 332 mm, from: Atlantic Coast of United States, South Carolina to Florida Straits. Two specimens, 198 and 310 mm, off South Carolina, Jan. 30, 1950, USNM 151958; 2, 260 and 265 mm, Combat St. 528, 31°18′N, 79°45′W, 100 fms., Oct. 9, 1957, BLBG; 1, 230 mm, Silver Bay St. 441, 27°39′N, 79°15′W, 275–300 fms., June 9, 1958, BLBG; 1, 294 mm, Combat St. 446, 25°10′N, 79°13′W, 250 fms., July 23, 1957, BLBG; 2, 175 and 332 mm, Combat St. 448, 24°04′N, 79°15′W, 250 fms., July 24, 1957, BLBG; 3, 290–308 mm, Oregon St. 1341, 22°55′N, 79°16′W, 240 fms., July 16, 1955, BLBG.

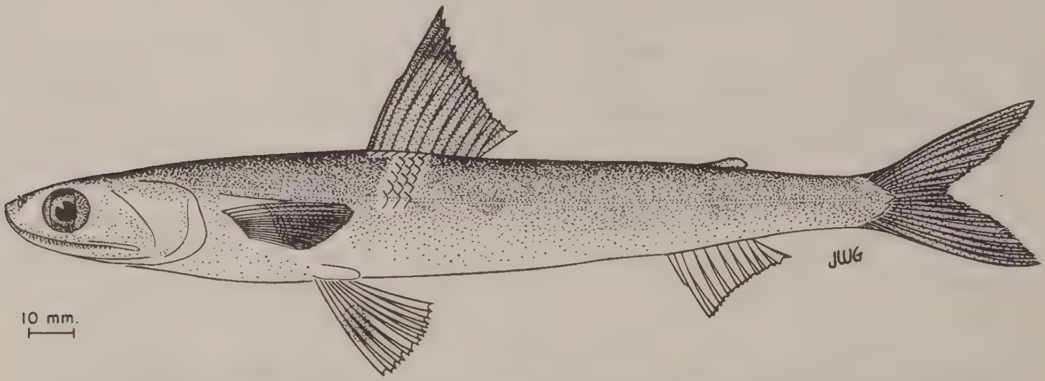

Figure 29. *Saurida normani,* 263 mm SL, off Savannah, Georgia, Combat St. 528, 31°18′N, 79°45′W, 100 fms., BLBG.

Gulf of Mexico and Caribbean Sea to Brazil. Three specimens, 142–162 mm, Silver Bay St. 312, 30°03′N, 86°50′W, 55 fms., March 16, 1958, BLBG; 1, 162 mm, Silver Bay St. 316, 29°50′N, 86°35′W, 60–75 fms., March 16, 1958, BLBG; 2, 165 and 217 mm, Oregon St. 944, 29°50′N, 86°30′W, 50 fms., March 21, 1954, UF 5194; 1, 169 mm, Pelican St. 144-2, 29°47′N, 86°52′W, 98 fms., March 5, 1939, USNM; 2, 260 and 270 mm, Oregon St. 2203, 29°13′N, 88°12′W, 125 fms., June 26, 1958, BLBG; 1, 115 mm, Oregon St. 733, 28°50′N, 85°43′W, 88 fms., Dec. 17, 1952, CNHM 45381; 1, 177 mm, Silver Bay St. 438, 23°36N, 87°54′W, 68 fms., May 18, 1958, BLBG; 1, 210 mm, Silver Bay St. 431, 23°13′N, 89°00′W, 57–60 fms., May 17, 1958, BLBG; 1, 79 mm, Oregon St. 1876, 16°45′N, 81°53′W, 100 fms., Aug. 22, 1957, CNHM 64443; 3, 200–240 mm, Oregon St. 1868, 16°36′N, 82°37′W, 175 fms., Aug. 21, 1957, BLBG; 1, 152 mm, Oregon St. 1904, 11°34′N, 83°07′W, 125 fms., Sept. 10, 1957, BLBG; 1, 256 mm, Oregon St. 1983, 09°53′N, 59°53′W, 125 fms., Nov. 3, 1957, BLBG; 1, 140 mm, Oregon St. 2225, 08°32′N, 59°10′W, 22–25 fms., Aug. 28, 1958, BLBG; 1, 215 mm, Oregon St. 2015, 07°38′N, 54°11′W, 75 fms., Nov. 8, 1957, BLBG; 2, 153 and 223 mm, OREGON St. 2013, 07°30′N, 54°16′W, 125 fms., Nov. 8, 1957, BLBG; 4, 124–130 mm, OREGON St. 2021, 07°18′N, 53°32′W, 100 fms., Nov. 8, 1957, BLBG; 2, 75 and 90 mm, OREGON St. 2268, 06°53′N, 55°59′W, 23 fms., Sept. 2, 1958, BLBG.

Distinctive Characters. See *Key to Atlantic Species*, p. 85.

Description. Proportional dimensions in per cent of standard length, with ranges given first, followed by the mean in parentheses, based on measurements from 11 specimens: 75, 90, 126, 130, 152, 169, 217, 256, 294, 308, and 332 mm SL.

Body at base of pelvic fin: depth 11.7–15.1 (13.7); width 11.7–15.0 (13.3).

Head: length 22.7–26.7 (25.1).

Snout: length 4.2–5.7 (5.1).

Eye: diameter 4.7–6.3 (5.5).[22]

Interorbital: width 4.9–5.7 (5.2).

Premaxillary: length 15.7–18.2 (17.0).

Distance from snout to origin of: dorsal fin 37.5–43.4 (41.0); anal fin 72.3–77.0 (74.9); pelvic fin 32.2–39.3 (36.5).

Distance from: origin of dorsal fin to origin of adipose fin 37.7–42.3 (40.0); tip of pectoral fin to origin of pelvic fin +2.0 to +6.5 (+4.0).

Dorsal fin: length of base 11.3–15.1 (12.8); length of longest ray 16.4–20.0 (18.9); length of last ray 4.6–7.0 (5.9).

Anal fin: length of base 7.7–9.5 (8.8).

Pectoral fin: length of longest ray 12.1–15.7 (14.6).

Pelvic fin: length of first ray 12.4–14.3 (13.3); length of longest ray 12.6–16.2 (14.1).[23]

Counts, based on 37 specimens.

Scales: predorsal 13–17 (2 specimens with 13, 4 with 14, 6 with 15, 16 with 16, 5 with 17); rows of complete scales between lateral line and base of dorsal fin 4 (all specimens).

Lateral-line scales: 51–56 (6 with 51, 8 with 52, 6 with 53, 9 with 54, 3 with 55, 2 with 56).

Fin rays: dorsal fin 10–12 (1 with 10, 18 with 11, 17 with 12); anal fin 9–11 (5 with 9, 26 with 10, 5 with 11); pectoral fin 13 or 14 (14 with 13, 23 with 14).

BODY depth and width at origin of pelvic fins about equal. SCALES of moderate size; pectoral axillary scale very long and pointed; small scales over the caudal rays of large specimens but absent on small specimens.[24] SNOUT length about equal to eye diameter. ADIPOSE EYELID wide. NOSTRILS placed well forward on the snout. LOWER JAW shorter than upper jaw, its tip not visible from above when mouth is closed. DORSAL fin origin about equidistant between adipose fin and tip of snout, generally nearer to adipose fin on specimens less than about 150 mm SL, and closer to tip of snout on larger specimens. ANAL base shorter than dorsal base, its length 57.4–67.9 % of dorsal base length.

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[22] Longley's report (*48*: 87) that eye diameter is less than interorbital width is in error, and that the distance from dorsal origin to tip of upper jaw is less than that from dorsal origin to origin of adipose fin applies only to large specimens.

[23] The assertion by Longley and Hildebrand (*49*: 229) that the pelvic is a little shorter than the pectoral is correct for specimens 126 mm SL and larger, but the reverse is true for specimens 90 mm SL and smaller.

[24] The scales do not have spinous, almost denticulate borders as described by Longley and Hildebrand (*49*: 228).

PECTORAL fins with tips extending much beyond origin of pelvic fins, but seldom reaching past origin of dorsal fin. PELVIC rays about equal in length. VERTEBRAE about 49.[25]

Color. In preservative, adults (Fig. 29) greyish on upper part of head, back, and down the sides to about the lateral line. Five or six faint darker blotches along lateral line from origin of dorsal to caudal peduncle. Sides of body below lateral line with some pigment, shading to a silvery belly. Dorsal and caudal fins dusky; upper two-thirds of pectoral dusky; a small patch of pigment about center of pelvic fin; anal fin pale.

Size. The largest specimen examined, and the largest on record, is 332 mm SL, captured in 250 fathoms.[26]

Habits. This species apparently is primarily an inhabitant of bottom offshore areas of the continental shelves and slopes and does not at any size frequent inshore areas. Extensive trawling records from the PELICAN, OREGON, COMBAT, and SILVER BAY indicate a depth distribution of 22 to 300 fathoms. The depth record for the species is from a trawl haul made at 275 to 300 fathoms—a 230-mm SL specimen from off eastern central Florida.

The behavior, food, and enemies are essentially unknown, but digenetic trematodes have been recorded from this species at Dry Tortugas, Florida (*51*: 358).

Relationship to Extralimital Species. Saurida normani with an included lower jaw is similar in this character to all of the Indo-Pacific species of *Saurida*. Based on key characters and descriptions given by Norman (*60*), Matsubara (*53*), and Schultz (*69*), and on our determinations, *S. normani* differs from those species by the following characters: *S. normani* has fewer scales than *S. elongata* (51–56 in lateral line and 13–17 predorsal in *S. normani*; about 59–66 and 20–26, respectively, in *S. elongata*). *S. normani* differs from *S. undosquamis* and *S. longimanus* in averaging more lateral-line scales (51–56 in *S. normani*; about 45–53 in *S. undosquamis*; about 45–49 in *S. longimanus*) and a shorter pectoral length (about 45–66 % of head length in *S. normani*; about 60–83 % in *S. undosquamis*; about 114–125 % in *S. longimanus*); and the longest dorsal ray averages a shorter length in *S. normani* than in *S. undosquamis* (about 65–80 % of head length in *S. normani*; about 80–100 % in *S. undosquamis*). In *S. normani* the pectorals extend much beyond the pelvic origins whereas in *S. gracilis* they reach or extend just beyond. Comparison of *S. normani* with published accounts of *S. tumbil* is difficult due to conflicting characters that have been given for the latter species. For *S. tumbil*, Norman (*60*) listed predorsal scales 16–19, pectoral length 47.6–55.6 % of head length (converted), and pectorals not, or only just, reaching the pelvic bases; Matsubara (*53*) recorded, respectively, 20–23, 59.2–74.6 % of head length (converted), and pectorals reaching to, or extending beyond, pelvic bases. Apparently *S. normani* averages a lower dorsal fin than *S. tumbil* (longest dorsal ray about 65–80 % of head length in *S. normani*; about 77–116 % in *S. tumbil*); elongation of the anterior dorsal rays, as occurs in large males of *S. tumbil*, has not been demonstrated for *S. normani*.

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[25] Longley and Hildebrand (*49*: 228) recorded about 31 + 18.

[26] The holotype reported by Longley and Hildebrand (*49*: 229) as 380 mm in length is 320 mm SL.

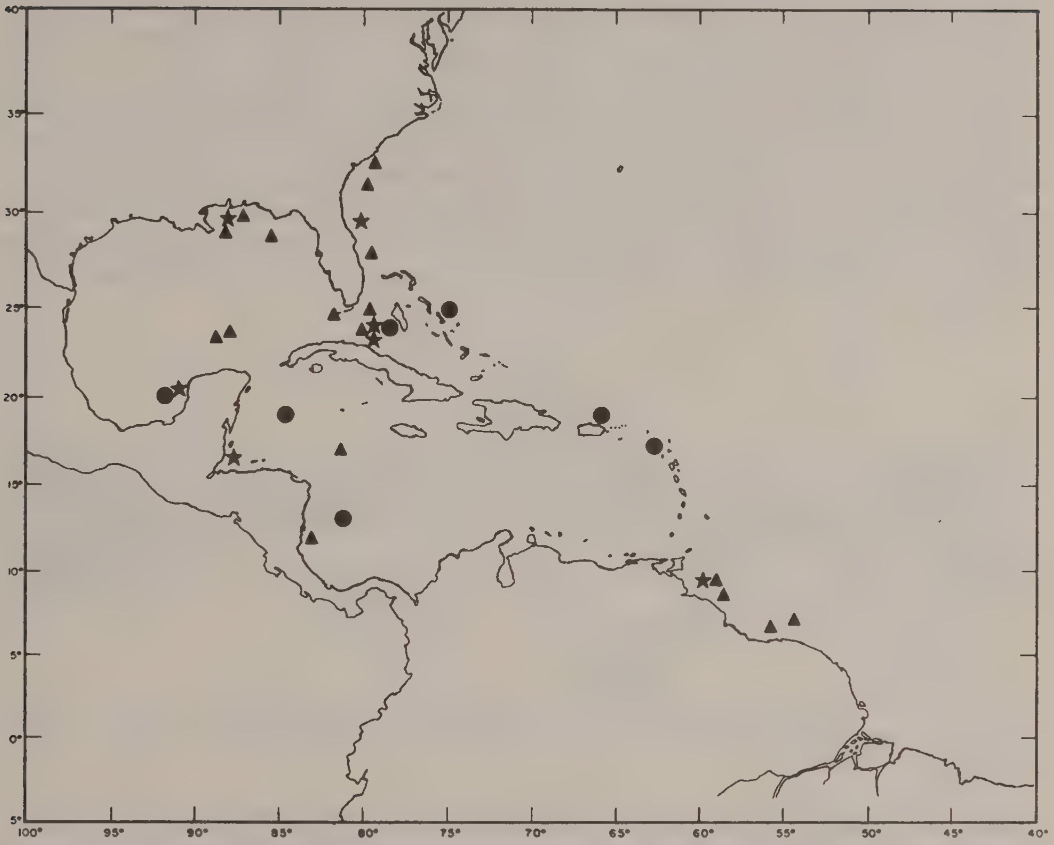

FIGURE 30. Distribution of *Saurida normani* (triangles), *Saurida suspicio* (circles), and *Saurida caribbaea* (stars).

Range. Fig. 30. The species was described from off Tortugas, Florida. Available records extend the range off the coast of the United States from South Carolina to the Florida Straits, and show that it is widespread in the Gulf of Mexico and the Caribbean Sea. Specimens were taken off the South American coast south to just below 07° N.

References:

Saurida normani Longley, Yearb. Carnegie Instn. Wash., *34*, 1935: 87 (not rare s. of Tortugas, Florida, from 60–100 fms.; type loc. s. of Tortugas, Florida; holotype USNM 107330, 320 mm SL); Longley and Hildebrand, Publ. Carnegie Instn. Wash., *32* (517), 1940: 228, fig. 2 (descr.; holotype designated by Hildebrand; Tortugas, Florida; 60–100 fms.); Longley and Hildebrand, Publ. Carnegie Instn. Wash., *34* (535), 1941: 24 (ref.; Tortugas, Florida); Manter, Amer. Midland Nat., *38* (2), 1947: 358, 374 (digenetic trematodes; Tortugas, Florida); Buller, U.S. Fish Wild. Serv., Sp. Sci. Rep. Fish. 58, 1951: 12 (S. Atlantic U.S.); Springer and Bullis, U.S. Fish. Wildl. Serv., Sp. Sci. Rep. Fish. 196, 1956: 53 (OREGON Sts. in Gulf of Mexico; rec. confirmed for St. 733 and 944); Briggs, Bull. Fla. State Mus., Biol. Sci., *2* (8), 1958: 257 (range); Gibbs, Copeia, 1959: 235, fig. 1 G (larvae descr.).

Saurida brasiliensis Norman 1935

Figures 12, 23, 31, 32

Study Material. A total of 173 specimens ranging in length between 21 and 102 mm, from: Atlantic Coast of the United States, North Carolina to Florida Straits. Two specimens, 56 and 70 mm, Combat St. 385, 34°46′N, 75°37′W, 50 fms., June 17, 1957, BLBG; 1, 79 mm, Combat St. 389, 34°36′N, 75°39′W, 30 fms., June 18, 1957, BLBG; 1, 60 mm, Pelican St. 195-6, 31°57′N, 79°29′W, 37 fms., March 13, 1940, USNM; 1, 68 mm, Pelican St. 195-7, 31°50′N, 79°26′W, 45 fms., March 13, 1940, USNM; 1, 70 mm, Pelican St. 197-7, 31°09′N, 80°09′W, 23 fms., March 15, 1940, USNM; 1, 64 mm, Pelican (new) St. 51, 29°48′N, 80°09′W, 190–202 fms., May 12, 1956, BLBG; 2, 53 and 75 mm, Combat St. 336, 29°10′N, 80°19′W, 25 fms., June 1, 1957, BLBG; 2, 53 and 60 mm, Combat St. 457, 25°16′N, 80°07′W, 65 fms., July 26, 1957, BLBG; 2, 76 and 77 mm, off Florida, 1931, USNM 117255; 3, 64–78 mm, Albatross, off Florida, April 9, 1886, USNM 131299; 3, 60–67 mm, Oregon St. 1345, 22°50′N, 79°18′W, 225 fms., July 17, 1955, CNHM 64056.

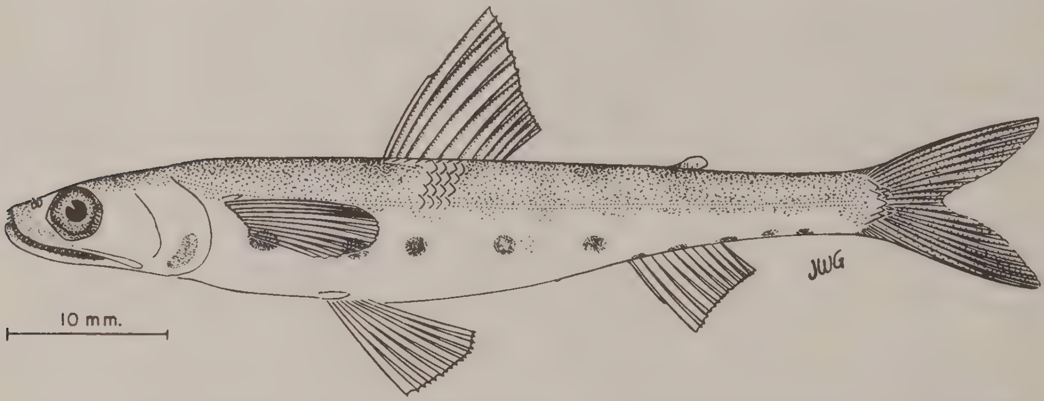

Figure 31. *Saurida brasiliensis*, 53.0 mm SL, off Daytona Beach, Florida, Combat St. 336, 29°10′N, 80°19′W, 25 fms., BLBG.

Gulf of Mexico, and Caribbean Sea to Brazil. Three specimens, 47–95 mm, Pelican St. 71-4, 29°34′N, 88°23′W, 25 fms., May 23, 1938, USNM; 2, 30 and 66 mm, Pelican St. 71-6, 29°29′N, 88°26′W, 30 fms., May 23, 1938, USNM; 4, 41–82 mm, Pelican St. 71-7, 29°29′N, 88°31′W, 29 fms., May 23, 1938, USNM; 1, 39 mm, 29°27′N, 87°48′W, March 4, 1885, USNM 129816; 4, 34–94 mm, Pelican St. 72-1, 29°27′N, 88°38′W, 26 fms., May 23, 1938, USNM; 8, 73–98 mm, Pelican St. 72-3, 29°17′N, 88°38′W, 35 fms., May 23, 1938, USNM; 2, 82 and 82 mm, Pelican St. 8, 29°10′N, 88°42′W, 45 fms., Feb. 3, 1938, USNM; 2, 53 and 75 mm, Pelican St. 83-3, 28°47′N, 91°49′W, 14 fms., July 12, 1938, USNM; 25, 53–75 mm, Albatross, 28°44′N, 85°16′W, March 15, 1885, USNM 134059; 1, 69 mm, Oregon St. 847, 28°44′N, 89°33′W, 53 fms., Oct. 24, 1953, UF 5197; 7, 52–97 mm, Pelican St. 83-4, 28°43′N, 91°49′W, 16 fms., July 12, 1938, USNM; 5, 85–102 mm, Pelican St. 83-5, 28°39′N, 91°48′W, 18 fms., July 12, 1938, USNM; 1, 73 mm, Pelican St. 93-8, 28°33′N, 92°15′W, 24 fms., Nov. 13, 1938, USNM; 5, 65–79 mm, Pelican St. 93-9, 28°29′N, 92°15′W, 28 fms., Nov. 13, 1938, USNM; 1, 26 mm, Pelican St. 94-1, 28°27′N, 92°14′W, 29 fms., Nov. 13, 1938, USNM; 1, 72 mm, Silver Bay St. 179, 28°06′N, 91°09′W, 75–100 fms., Sept. 21, 1957, BLBG; 1, 91 mm, Pelican St. 39, 27°46′N, 96°51′W, 13 fms., April 20, 1938, USNM; 8, 51–85 mm, Pelican St. 42, *ca.* 27°45′N, 96°49′W, *ca.* 14 fms., April 22, 1938, USNM; 3, 65–87 mm, Pelican St. 42-2, 27°43′N, 96°44′W, 17 fms., April 22, 1938, USNM; 2, 81 and 96 mm, Pelican St. 110-3, 27°39′N, 96°49′W, 16 fms., Jan. 28, 1939, USNM; 3, 71–80 mm, Pelican St. 39–40, *ca.* 27°35′N, 96°30′W, *ca.* 30 fms., April 21, 1938, USNM; 3, 82–100 mm, Oregon St. 1080, 26°09′N, 97°05′W, 11 fms., June 2, 1954, UF; 9, 39–68 mm, Oregon St. 1086, 26°10′N, 96°54′W, 18 fms., June 3, 1954, UF 5238; 5, 52–83 mm, Oregon St. 1086, 26°10′N, 96°54′W, 18 fms., June 3, 1954, USNM; 5, 21–25 mm, Campeche Bank in lower Gulf of Mexico, Aug. 27, 1951, CNHM 64305; 2, 63 and 73 mm, Oregon St. 1057, 18°45′N, 93°15′W, 19 fms., May 16, 1954, USNM; 2, 77 and 85 mm, Oregon St. 2356, 17°33′N, 63°35′W, 125–132 fms., Sept. 25, 1958, BLBG; 10, 60–85 mm, Oregon St. 1876, 16°45′N, 81°53′W, 100 fms., Aug. 22, 1957, CNHM 64444; 1, 37 mm, Oregon St. 1866, 16°30′N, 83°30′W, 38 fms., Aug. 21, 1957, BLBG; 1, 37 mm, Old Providence I. (western Caribbean), March 24, 1941, ANSP 72747; 1, 75 mm, Oregon St. 2268, 06°53′N, 55°59′W, 23 fms., Sept. 2, 1958, BLBG; 1, 71 mm, Oregon St. 2041, 05°55′N, 52°46′W, 25 fms., Nov. 12, 1957, CNHM 64447.

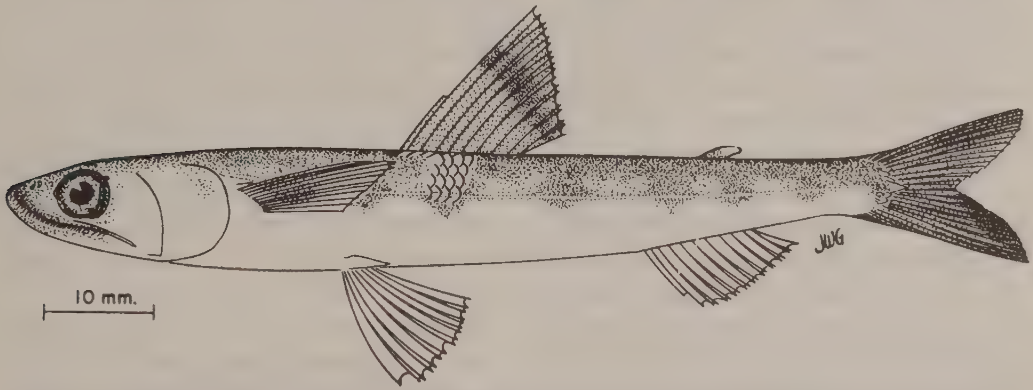

Figure 32. *Saurida brasiliensis*, 80.0 mm SL, western Caribbean Sea off Honduras, Oregon St. 1876, 16°45′N, 81°53′W, 100 fms., CNHM 64444.

West Africa. Five specimens, 52–59 mm, 0°53′S, 08°40′E, or 15 mi. S × W of Cap Lopez, west coast of Gabon, 33–35 m, March 8, 1949, BLBG; 16, 45–87 mm, 7° S, 12° E, or 42 mi. SW of Margate Head, 120 m, Nov. 8, 1948, BLBG; 4, 54–92 mm, 04°53′S, 11°38′E, or 12 mi. W × S of Pointe Noire, 70–80 m, March 28–29, 1949, BLBG.

Distinctive Characters. See *Key to Atlantic Species*, p. 85.

Description. Proportional dimensions in per cent of standard length, with ranges given first, followed by the mean in parentheses, based on measurements from 12 specimens: 26, 34, 52, 53, 56, 70, 75, 79, 87, 95, 96, and 98 mm SL.

Body at base of pelvic fin: depth 9.2–15.5 (12.7); width 8.5–13.8 (11.8).

Head: length 22.4–26.5 (24.4).

Snout: length 4.4–6.3 (5.6).

Eye: diameter 4.4–6.3 (5.5).

Interorbital: width 2.6–5.0 (3.4).

Premaxillary: length 13.8–19.6 (16.1).

Distance from snout to origin of: dorsal fin 43.2–46.2 (44.4); anal fin 70.3–74.0 (72.0); pelvic fin 37.0–39.2 (38.4).

Distance from: origin of dorsal fin to origin of adipose fin 32.5–37.0 (35.0); tip of pectoral fin to origin of pelvic fin +4.7 to +10.1 (+8.0).

Dorsal fin: length of base 12.6–15.9 (14.2); length of longest ray 19.2–26.2 (21.4); length of last ray 5.3–7.4 (6.4).

Anal fin: length of base: 10.8–12.7 (11.6).

Pectoral fin: length of longest ray 16.3–23.5 (19.2).

Pelvic fin: length of first ray 11.7–17.6 (14.9); length of longest ray 12.1–18.5 (16.5).

Counts, based on 118 specimens.

Scales: predorsal 12–19 (1 specimen with 12, 0 with 13, 4 with 14, 16 with 15, 36 with 16, 34 with 17, 12 with 18, 6 with 19); rows of complete scales between lateral line and base of dorsal fin 3–4 (79 with 3, 26 with 3 or 4, 7 with 4).

Lateral-line scales: 43–49 (2 with 43, 6 with 44, 21 with 45, 18 with 46, 42 with 47, 22 with 48, 4 with 49), 40 (*50*: 24) to 50 (*66*: 79) reported.

Fin rays: dorsal fin 9–12 (1 with 9, 38 with 10, 69 with 11, 1 with 12), 13 reported (*66*: 79); anal fin 10–13 (9 with 10, 50 with 11, 48 with 12, 2 with 13); pectoral fin 11–13 (41 with 11, 69 with 12, 8 with 13).

Body depth at origin of pelvic fins a little greater than width. Scales large; pectoral axillary scale moderate in size. Snout length equal to eye diameter. Adipose eyelid narrow. Nostrils placed about midway on the snout. Lower jaw extending beyond upper jaw and plainly visible from above when mouth is closed. Dorsal fin origin considerably closer to adipose fin than to tip of snout. Anal base shorter than dorsal base, its length 69.1–92.5 % of dorsal base length. Pectoral fins with tips extending much beyond origin of pelvic fin, sometimes extending well past origin of dorsal fin. Pelvic rays about equal in length, the first ray equal to, or slightly shorter, than longest ray. Vertebrae 44.[27]

Color. In preservative, adults (Fig. 32) brownish on upper part of head, back, and sides down to about the lateral line. A faint saddle of brown at origin of dorsal fin, one at posterior end of dorsal fin base, and one just anterior to adipose fin. About 6 faint blotches of brown along lateral line. Lower side of head, lower parts of sides, and belly pale. Dorsal and anal fins dusky; a few spots of pigment on lower portion of pectorals; pelvic and anal fins pale. Pattern in young less distinct. Lateral paired pigment spots of larvae faintly discernible at 53 mm (Fig. 31).

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[27] Longley and Hildebrand (50: 24) reported the vertebrae of one specimen as 26 + 18.

Size. The largest specimen examined was 102 mm SL, taken in 18 fathoms of water. Specimens up to 115 mm SL have been reported from off Tortugas, Florida (*50*: 24), and specimens up to 170 mm TL have been recorded from off West Africa (*66*: 79).

Habits. This apparently is an inhabitant of offshore bottom areas of the open ocean and does not at any size inhabit shore areas. The extensive trawling records from the PELICAN, OREGON, COMBAT, and SILVER BAY indicate a depth distribution from about 10 to 225 fathoms, but with a great majority of records from less than 100 fathoms. The depth record for the species is 225 fathoms—60–67-mm specimens from north of Central Cuba.

The species was reported to be sexually mature in late August at 80 mm TL at Tortugas, Florida (*50*: 24). From specimens taken off West Africa, evidence was found of gonad maturation at sizes larger than 82 mm TL, with females averaging a larger mean size than males, and specimens 74 mm and smaller being immature (*66*: 79).

Relationship to Extralimital Species. Saurida brasiliensis differs from all of the Indo-Pacific species of *Saurida* in having the lower jaw longer than the upper jaw.

Synonymy. When Norman described *Saurida brasiliensis* from three specimens taken off Brazil and *S. parri* from twelve specimens collected off Angola and French Congo, West Africa (*60*: 126, Fig. 5), he indicated that the two were closely related but separate because *brasiliensis*, compared with *parri*, had fewer lateral-line scales (43–47 in *brasiliensis vs.* 48–50 in *parri*), had fewer pectoral rays (11 or 12 *vs.* 13), and had a more strongly upturned lower jaw than *parri*. In 100 specimens of *S. brasiliensis* from the western North Atlantic and 25 from off French Equatorial Africa, we found ranges of 43–49 lateral-line scales and 11–13 pectoral rays in *brasiliensis* and 48–51 lateral-line scales and 12 or 13 pectoral rays in *parri*. We find no appreciable difference in the upturning of the lower jaws in the two series of specimens. Although the West African specimens averaged a greater number of scales in the lateral line and of rays in the pectoral fin, the overlap is such that identification to species is not possible with these characters. Therefore we consider *S. parri* a synonym of *S. brasiliensis*.

Range. Fig. 23. The species was for many years unrecorded north of the Florida Keys. Available records extend the range along the coast of the United States from North Carolina to Florida, across the northern Gulf of Mexico, the lower Gulf of Mexico, and into the western Caribbean Sea. Specimens were also taken off the South American coast to about 05° N. It has been recorded off West Africa from the equator to about 13° S and at Ascension Island (*66*: 79).

Synonyms and References:

Trachinocephalus myops (*non* Forster), Regan, Rep. Brit. Antarctic Exped. 1910, *1* (1), 1914: 22 (22°56′S, 41°34′W, off Cape Frio, Brazil; *fide* Norman's [1935: 125] exam. of the spec.).

Saurus spec. juv., Metzelaar, Rapp. Bet. Voor. Ind. Zee. Kol. Curaçao, *2* (2), 1919: 23 (descr.; Trinidad; *fide* Norman's [1935] exam. of spec. in AMNH).

Saurida brasiliensis Norman, Proc. zool. Soc. London, 1935: 125, fig. 14 (type loc. of 80-mm holotype, off Cape Frio, Brazil; of 38 and 40-mm paratypes, Trinidad; holotype in BMNH; paratypes in AMNH); Longley, Yearb. Carnegie Instn. Wash., *34*, 1935: 87 (*cf. S. normani*); Longley and Hildebrand, Publ. Carnegie Instn. Wash., *32* (517), 1940: 229 (*cf. S. normani*); Longley and Hildebrand, Publ. Carnegie Instn. Wash., *34* (535), 1941: 23 (descr.; s. of Tortugas, Florida); Fowler, Arqu. Zool. Estad. São Paulo, *3* (6), 1941: 140 (Brazil); Fowler, Notulae Nat., *246*, 1952: 2 (SW and SE of Sombrero Key Light, Florida, in 40 and 70 fms. respectively); Hildebrand, Publ. Inst. Mar. Sci. Texas, *3* (2), 1954: 289, 290 (north. Gulf coast of Mexico; off Corpus Christi Pass and Padre I., Texas); Springer and Bullis, U.S. Fish Wildl. Serv., Sp. Sci. Rep. Fish. 196, 1956: 53 (OREGON Sts. in the Gulf of Mexico; record confirmed for St. 1081). Briggs, Bull. Fla. State Mus., Biol. Sci., *2* (8), 1958: 257 (range); Gibbs, Copeia, 1959: 235, fig. 1 F (larvae descr.).

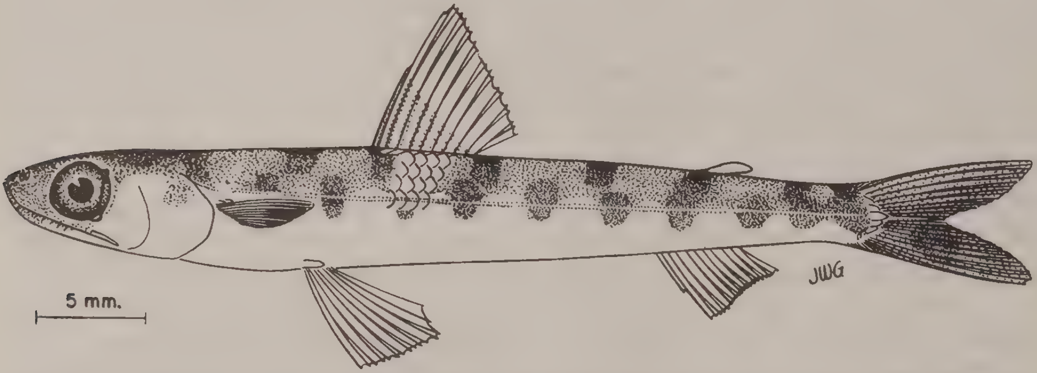

FIGURE 33. *Saurida suspicio*, 39.5 mm SL, Andros Island, Bahamas, Chaplin Bahaman Shore Fish Program, St. 396, ANSP (uncatalogued).

Saurida parri Norman, Proc. zool. Soc. London, 1935: 126, fig. 15 (type loc. of holotype, 115 mm, and of 1 paratype, 37 mm, off St. Paul de Loanda, Angola, 35–36 fms.; of 10 more paratypes, 80–125 mm, off Cape Lopez, French Congo, 31–37 fms.; types in BMNH.) Norman, 'Discovery' Rep., 7, 1935: 9 (type spec. relisted); Poll, Résult. Scl. exped. océanogr. Belge eaux côt. Afr. Atlant. sud (1948–1949), *4* (2), 1953: 76, fig. 34 (descr.; weights; many localities, Equatorial W. Africa); Springer and Bullis, U.S. Fish Wildl. Serv., Sp. Sci. Rep. Fish. 196, 1956: 54 (OREGON St. 1345, 22°50′N, 79°18′W).

Saurida suspicio Breder 1927

Figures 13, 30, 33, 34

Study Material. A total of 7 specimens ranging in length between 32 and 74 mm, from: Three specimens, 39–43 mm, Andros I., Bahamas, July 12, 1957, Chaplin Bahaman Shorefishes Program, ANSP; 1, 57 mm, FISH HAWK, near San Juan, Puerto Rico, 1898–1899, USNM 76512; 1, 74 mm, CAROLINE, West Indies, March 1, 1933, USNM 108441; 1, 32 mm, PAWNEE, Misteriosa Bank, Caribbean Sea, April 10, 1925, BOC 111; 1, 58 mm, OREGON, 2 mi. W. of Catalina Harbor, Old Providence I., Colombia, dip net, Aug. 29, 1957, BLBG.

Distinctive Characters. See *Key to Atlantic Species,* p. 85.

Description. Proportional dimensions in per cent of standard length, with ranges given first, followed by the mean in parentheses, based on measurements from 7 specimens: 32, 39, 43, 43, 57, 58, and 74 mm SL.

Body at base of pelvic fin: depth 12.4–15.5 (14.1); width 9.7–13.0 (11.7).

Head: length 25.6–26.7 (26.1).

Snout: length 5.1–7.4 (6.1).

Eye: diameter 6.2–7.8 (7.1).

Interorbital: width 2.0–3.2 (2.6).

Premaxillary: length 13.8–19.0 (16.7).

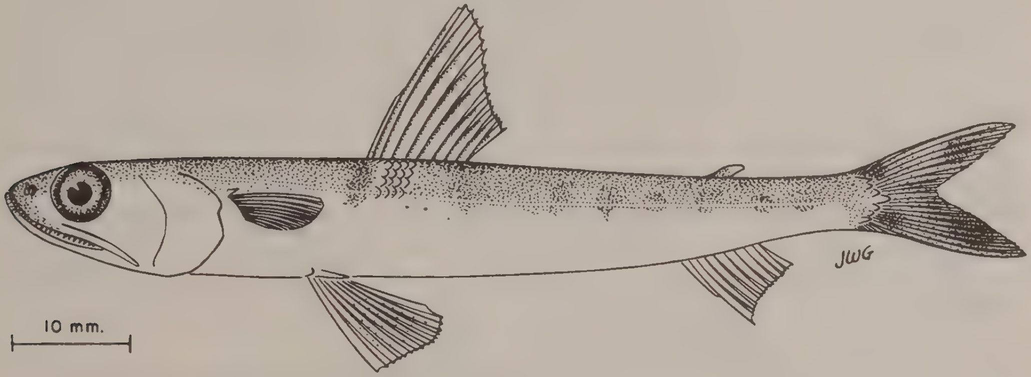

FIGURE 34. *Saurida suspicio,* 74.1 mm SL, Virgin Islands, M.V. CAROLINE, USNM 108441.

Distance from snout to origin of: dorsal fin 41.9–46.9 (43.4); anal fin 73.8–77.2 (75.3); pelvic fin 35.1–39.8 (37.3).

Distance from: origin of dorsal fin to origin of adipose fin 36.0–40.6 (38.4); tip of pectoral fin to origin of pelvic fin 0 to +1.6 (+0.4).

Dorsal fin: length of base 10.7–14.1 (12.0); length of longest ray 19.5–20.9 (20.1), up to 22 reported[28]; length of last ray 5.6–6.7 (6.3).

Anal fin: length of base 8.6–11.9 (9.8).

Pectoral fin: length of longest ray 10.9–12.8 (11.6).

Pelvic fin: length of first ray 13.4–15.3 (14.4); length of longest ray 15.2–17.2 (16.4), up to 18 reported.[28]

Counts, based on 7 specimens.

Scales: predorsal 13–18 (1 specimen with 13, 0 with 14, 2 with 15, 1 with 16, 1 with 17, 2 with 18); rows of complete scales between lateral line and base of dorsal fin 3 (all specimens).

Lateral-line scales: 52 or 53 (5 with 52, 2 with 53), 55 and 56 reported.[28]

Fin rays: dorsal fin 10 or 11 (5 with 10, 2 with 11); anal fin 10–12 (2 with 10, 4 with 11, 1 with 12); pectoral fin 11 or 12 (5 with 11, 2 with 12), 13 reported (60).

BODY depth at base of pelvic fin averaging but little more than width. SCALES moderate; pectoral axillary scale moderate in size. SNOUT usually shorter than eye, but occasionally larger than eye. Adipose eyelid moderate in size. Nostrils placed well forward on snout. Lower jaw longer than upper jaw and visible from above when the mouth is closed. Dorsal fin origin closer to adipose fin than to tip of snout. Anal base shorter than dorsal base, its length 67.9–92.7 $^0/_0$ of dorsal base length. Pectoral fins with tips extending to, or just beyond, origin of pelvic fin, not extending to origin of dorsal fin. Pelvic rays not quite equal in length, the first ray always a little shorter than longest ray (7th).

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[28] Parr (65: 8) reported on specimens 66, 74, and 74 mm SL.

Color. In preservative, adults (Fig. 34) light brownish on upper part of head, on back, and down the sides to about the lateral line. Six faint saddles of reddish brown over the back, the 1st just anterior to origin of dorsal fin, the 2nd at origin of dorsal fin, 3rd at posterior end of dorsal fin base, the 4th about midway between dorsal and adipose fins, the 5th at origin of adipose fin, and the 6th on the caudal peduncle. In addition, usually 8–10 spots along lateral line. Sides of head, lower sides of body, and belly pale. Mandible tip dusky. Dorsal fin dusky; only a few pigment spots on pelvic fins; anal and pectoral fins clear; caudal dusky with darker patches on inner parts of both lobes. Basic adult color pattern much more pronounced in the young (Fig. 33).

Size. The largest specimen we examined was 74 mm SL. The holotype and largest specimen was recorded as 75 mm SL or 86 mm TL (*10*: 15). This is apparently the smallest of our lizardfishes, and also the least common.

Habits. S. suspicio has been taken only from the surface or in shallow water near shore or over reefs.[29]

Relationship to Extralimital Species. Saurida suspicio differs from all of the Indo-Pacific species of *Saurida* in having the lower jaw longer than the upper jaw.

Range. Figure 30. The species was described from material taken on the Misteriosa Bank in the northern Caribbean Sea. There are now records from the Bahamas, Puerto Rico, the Leeward Islands, and Old Providence Island off Colombia. This indicates a rather limited range associated with the Bahamas, West Indies, and Caribbean Sea.

Synonyms and References:

Saurida tumbil (*non* Bloch), Metzelaar, Rapp. Bet. Voor. Ind. Zee. Kol. Curaçao, *2* (2), 1919: 24 (descr.: St. Eustatius, Dutch W. Indies; *fide* Norman's [1935] exam. of spec. in AMNH).

Saurida suspicio Breder, Bull. Bingham oceanogr. Coll., *1* (1), 1927: 15, figs. 8, 9 (type loc. Misteriosa Bank, Caribbean Sea; type BOC 62; also one paratype from same loc.); Parr, Bull. Bingham oceanogr. Coll., *3* (4), 1930: 4, 7 (descr.; *cf.* other *Saurida* spp.; Cat I., Bahamas); Shanklin, Acta zool., Stockholm, *15* (2/3), 1934: 410 (cerebellum and cerebellar pathways; Bahama Is.); Shanklin, Philos. Trans. roy. Soc. London, (B) *224* (516), 1935: 361 (descr. brain cell areas and fiber pathways; off Cat I., Bahamas); Norman, Proc. zool. Soc. London, 1935: 124, 125 (key; descr.; St. Eustatius, Leeward Is.); Longley, Yearb. Carnegie Instn. Wash., *34*, 1935: 87 (*cf. S. normani*); Longley and Hildebrand, Publ. Carnegie Instn. Wash., *32* (517), 1940: 229 (*cf. S. normani*); Fowler, Monogr. Acad. nat. Sci. Philad., *6*, 1944: 438 (Bahamas after Parr 1930), 459 (Misteriosa Bank, after Breder 1927); Gibbs, Copeia, 1959: 235, fig. 1 H (larvae descr.).

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[29] The holotype and paratypes were taken at the surface (*10*: 15), and a specimen was taken from between 4 and 5 fathoms off St. Eustatius (*57*: 23).

Saurida caribbaea Breder 1927

Figures 30, 35

Study Material. A total of 21 specimens ranging in length between 53 and 130 mm, from: Atlantic Coast of United States, Northern Florida to Florida Straits; Gulf of Mexico; West Indies; Northwestern Caribbean Sea; and off South America to about 09°N.

One specimen, 94 mm, Combat St. 480, 29°30′N, 80°08′W, 210 fms., Aug. 17, 1957, BLBG; 3, 53–76 mm, Combat St. 448, 24°04′N, 79°15′W, 250 fms., July 24, 1957, BLBG; 1, 119 mm, Gulf of Mexico (Florida), Dec. 8, 1955, USNM 158844; 1, 130 mm, Oregon St. 1804, 30°11′N, 88°28′W, 3 fms., May 31, 1957, USNM 158843; 1, 88 mm, Oregon St. 446, 20°05′N, 91°28′W, 17 fms., Aug. 26, 1951, BLBG; 1, 91 mm, West Indies, March 3, 1933, USNM 108443; 1, 106 mm, West Indies, March 4, 1933, USNM 108440; 2, 64 and 109 mm, Pawnee, N. of Glover Reef, NW. Caribbean Sea, 48 fms., April 20, 1925, BOC 110; 2, 100 and 102 mm, Oregon St. 1341, 22°55′N, 79°16′W, 240 fms., July 16, 1955, BLBG; 5, 63–95 mm, Oregon St. 1989, 09°45′N, 59°45′W, 100–200 fms., Nov. 4, 1957, CNHM 64445 and 64446; 3, 53–91 mm, Oregon St. 1989, 09°45′N, 59°45′W, 100–200 fms. Nov. 4, 1957, BLBG.

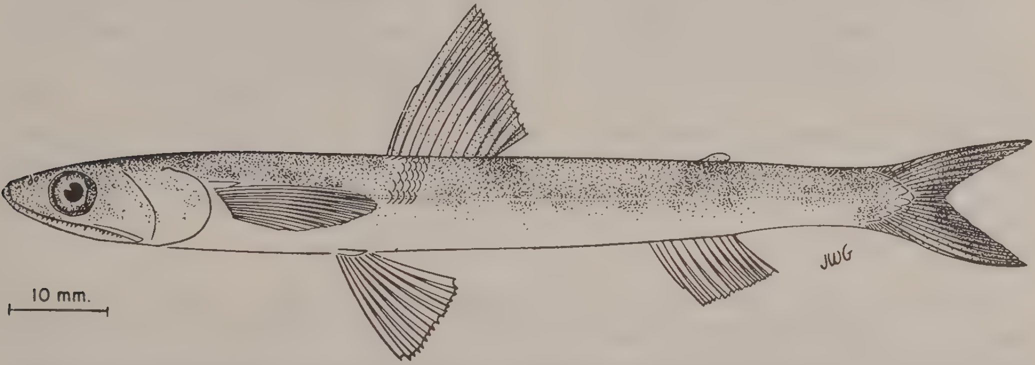

Figure 35. *Saurida caribbaea*, 89.0 mm SL, off Venezuela, Oregon St. 1989, 09°45′N, 59°45′W, BLBG.

Distinctive Characters. See *Key to Atlantic Species*, p. 85.

Description. Proportional dimensions in per cent of standard length, with ranges given first, followed by the mean in parentheses, based on measurements from 9 specimens: 83, 88, 89, 91, 91, 100, 102, 106, and 119 mm SL.

Body at base of pelvic fin: depth 9.3–13.2 (11.2); width 9.3–12.6 (10.7).

Head: length 23.0–24.6 (23.8).

Snout: length 4.8–7.3 (6.1).

Eye: diameter 4.9–6.6 (5.5).

Interorbital: width 2.6–3.6 (3.0).

Premaxillary: length 15.5–18.7 (16.9).

Distance from snout to origin of: dorsal fin 43.7–46.4 (44.4); anal fin 72.8–75.3 (73.9); pelvic fin 37.5–40.2 (38.8).

Distance from: origin of dorsal fin to origin of adipose fin 33.1–36.8 (35.1); tip of pectoral fin to origin of pelvic fin +4.6 to +7.8 (+6.1).

Dorsal fin: length of base 10.6–13.8 (12.3); length of longest ray 18.9–21.6 (20.1); length of last ray 4.5–6.7 (5.8).

Anal fin: length of base 9.0–12.0 (10.3).

Pectoral fin: length of longest ray 17.5–20.0 (18.2).

Pelvic fin: length of first ray 14.6–16.5 (15.4); length of longest ray 14.7–16.6 (15.6).

Counts, based on 21 specimens.

Scales: predorsal 18–21 (2 specimens with 18, 11 with 19, 5 with 20, 1 with 21); rows of complete scales between lateral line and base of dorsal fin 4 (all specimens).

Lateral-line scales: 54–60 (5 with 54, 3 with 55, 5 with 56, 2 with 57, 4 with 58, 1 with 59, 1 with 60).

Fin rays: dorsal fin 10–12 (3 with 10, 16 with 11, 2 with 12); anal fin 11 or 12 (13 with 11, 8 with 12); pectoral fin 12 or 13 (1 with 12, 20 with 13).

Body depth and width at origin of pelvic fins about equal. Scales of moderate size; pectoral axillary scale moderate in size. Snout length about equal to eye diameter. Adipose eyelid moderate. Nostrils placed about midway on the snout. Lower jaw longer than upper jaw and visible from above when mouth is closed. Dorsal fin origin considerably closer to adipose fin than to tip of snout. Anal base usually shorter than, but sometimes about equal to, dorsal base, its length 70.8–97.1 % of dorsal base length. Pectoral fin with tip extending much beyond origin of pelvic fin, usually reaching to or past origin of dorsal fin. Pelvic rays about equal in length.

Color. In preservative, adults (Fig. 35) light brownish on upper part of head, back, and sides down to about the lateral line. Darker blotches on back, but these not saddle-like; irregular spots of darker brown on sides above lateral line, along lateral line, and just below it. Lower part of head, lower parts of sides, and belly pale with yellowish cast. Dorsal dusky with darker strip on distal portion; caudal dusky with inner portion of lower lobe the darkest; pectoral, pelvic, and anal fins pale.

Size. The largest specimen examined and the largest on record is 130 mm SL.

Habits. Apparently the species is primarily an inhabitant of bottom offshore areas of the continental shelves and slopes, although one large specimen was taken in a trap lift net from 3 fathoms. The depth record for the species is 250 fathoms—53- to 76-mm specimens from west of the Great Bahama Bank.

Relationship to Extralimital Species. Saurida caribbaea differs from all of the Indo-Pacific species of *Saurida* in having the lower jaw longer than the upper jaw.

Range. Fig. 30. The species was described from the Caribbean Sea off British Honduras. Available records extend the range off the coast of the United States from northeastern Florida to the Florida Straits, in the Gulf of Mexico, and off the South American coast south to about 09°N.

Synonyms and References:

Saurida caribbaeus Breder, Bull. Bingham oceanogr. Coll., *1* (1), 1927: 14, 16, figs. 7, 9 (type loc. N. of Glover Reef off British Honduras, 48 fms.; type BOC 57, 131 mm TL, 5 paratypes originally deposited there; one paratype, 123 mm, now in BMNH); Parr, Bull. Bingham oceanogr. Coll., *3* (4), 1930: 4 (*cf.* other *Saurida* spp.); Norman, Proc. zool. Soc. London, 1935: 99 (paratype donated to BMNH).

Saurida caribbaea, Norman, Proc. zool. Soc. London, 1935: 124, 127 (key; descr.; paratype from N. of Glover Reef off British Honduras in BMNH); Longley, Yearb. Carnegie Instn. Wash., *34*, 1935: 87 (*cf. S. normani*); Longley and Hildebrand, Publ. Carnegie Instn. Wash., *32* (517), 1940: 229 (*cf. S. normani*); Fowler, Monogr. Acad. nat. Sci. Philad., *6*, 1944: 459 (Misteriosa Bank, after Breder 1927).

Saurida caribbea, Gibbs, Copeia, 1959: 232 (ref.).

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Influence of Salinity on the Response of Estuarine Animals to Ionizing Radiation

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During investigations of the effects of ionizing radiation on estuarine animals we found that animals in water with different salinities respond differently to radiation. LD-50's and survival were determined for three euryhaline species after irradiation with cobalt-60 in water at different salinities within their tolerance ranges. Mummichog, *Fundulus heteroclitus,* were tested at salinities between 5-25‰; grass shrimp, *Palaemonetes pugio,* between 15-30‰; and brine shrimp, *Artemia salina,* between 5-100‰. Comparison of LD-50's at the salinities tested showed that mummichog and grass shrimp, typical estuarine species, were more resistant to radiation at lower salinities. The magnitude of variation between LD-50's of organisms at different salinities varies with temperature. The resistance of brine shrimp to radiation is not increased at lower salinities; rather, irradiated brine shrimp survive longer than unirradiated at 5‰. These data indicate that salinity has a significant role in determining the response of estuarine species to radiation.

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THE RELATION BETWEEN MOLECULAR STRUCTURE AND BIOLOGICAL ACTIVITY AMONG MONONITROPHENOLS CONTAINING HALOGENS

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and Manning A. Smith

ABSTRACT

The results of tests of the biological activity of certain nitrophenols containing halogens are reported. Some of these are shown to be significantly more toxic to larvae of the sea lamprey (*Petromyzon marinus* L.) than to fishes. It is proposed that the death of lamprey larvae exposed to these compounds results from an acute hypotension (shock) with concomitant circulatory and respiratory failure. Rainbow trout (*Salmo gairdneri*), on the other hand, appear to die, at higher concentrations of the toxin, due to a chemically-caused mechanical interference with respiration through the gills. A systematic series of studies of mononitrophenols containing halogens disclosed that those phenols having the nitro group in the *para*-position and a halogen atom or group in the *meta*-position are generally more toxic to lampreys than to fish. The halogens or halogen groups used in this study were fluorine, chlorine, bromine, and trifluormethyl. The same substituents in other positions only occasionally gave rise to selectively toxic compounds. The relationship between the selectively active class of nitrophenols containing halogens and other related structures is discussed.

Introduction

Efforts to control the parasitic sea lamprey (*Petromyzon marinus* L.) in the Great Lakes are directed at present to the applications of a selective toxicant (called variously a lampricide or lamprey larvicide) to streams inhabited by lamprey larvae. Since 1961, the larvicide that has been used almost exclusively in the control program has been 3-trifluor(o)methyl-4-nitrophenol (TFM)[1] (Fig. 1A). The biological activity of this chemical has

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[1] Chemical Abstracts name: α, α, α-trifluoro-4-nitro-*m*-cresol.

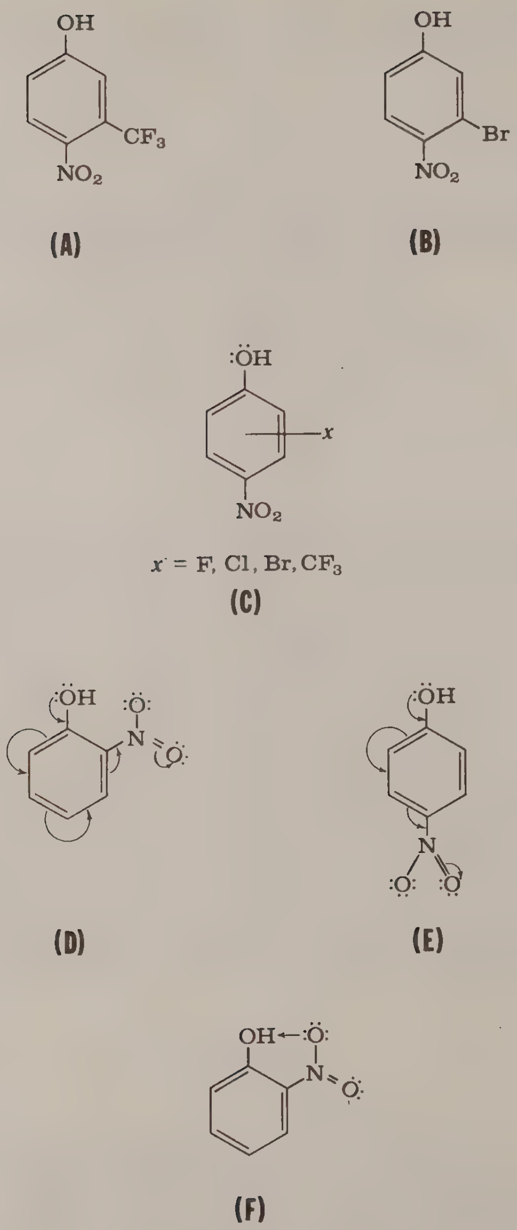
OH
CF3
NO2
(A)
OH
Br
NO2
(B)
:ÖH
x
NO2
x = F, Cl, Br, CF3
(C)
:ÖH
:Ö:
N
Ö:
(D)
:ÖH
N
:Ö:
:Ö
(E)
OH
:Ö:
N
Ö:
(F)

Figure 1. Halo-nitrophenols and nitrophenols: (A) 3-trifluormethyl-4-nitrophenol (TFM); (B) 3-bromo-4-nitrophenol; (C) 4-nitrophenols containing halogen(s); (D) 2-nitrophenol acidity enhancement by resonance interaction; (E) 4-nitrophenol acidity enhancement by resonance interaction; (F) 2-nitrophenol intramolecular hydrogen bonding.

been described by Applegate, Howell, and Smith (1958); Applegate, Howell, Moffett, Johnson, and Smith (1961); and, by Applegate and King (1962). Physical and chemical properties of the substance have been described by Smith, Applegate, and Johnson (1961) and methods of analysis for the purpose of controlling its application in natural waters have been described by Smith, Applegate, and Johnson (1960) and Kanayama (1963). This compound is, however, only one of about 15 closely related structures, all mononitrophenols containing halogens, that display, to a greater or lesser degree, a selectively toxic action upon lampreys. Applegate *et al.* (1958) have described the larvicidal properties of some of these compounds. Although not all of the mononitrophenols containing halogens (in fact, less than half of those tested) are selectively toxic to lampreys, no other "family" or group of related compounds has, to our knowledge, displayed any useful larvicidal activity except for the substituted nitro-salicylanilides which are reported upon by Starkey and Howell (1966) in another paper in this Report.

Between 1953 and 1957 a broad range of chemical substances was screened initially in an attempt to find a substance that would destroy larval sea lampreys without causing significant harm to any other animal life inhabiting the same waters. The results of these screening tests, presented by Applegate *et al.* (1957), included descriptions of the toxicity of a variety of phenolic compounds and their derivatives. It now appears not only possible, but also desirable, to review the findings of this and subsequent testing programs to demonstrate the relationship we found between the structure of phenolic compounds and their biological effects on lampreys and other fishes.

Although the phenols and their derivatives include some well-known herbicides and pesticides (*e.g.*, "2,4-D", "2,4,5-T", "2,4,5-TP", etc.), there appears to be a scarcity, if not total absence, of published reports describing any selectively toxic action of this group of compounds among the different classes of chordates except for the following disclosures: Applegate and Howell, United States Patents No. 2,821,499 (Jan. 28, 1958), No. 3,219,521 (Nov. 23, 1965) and Dominion of Canada Patents No. 600,326 (June 21, 1960), No. 665,469 (June 25, 1963), and No. 683,165 (Mar. 31, 1964); Howell and King, United States Patents No. 3,238,098 (Mar. 1, 1966) and No. 3,271,246 (Sept. 6, 1966); Pyne, United States Patent No. 3,052,601 (Sept. 4, 1962); and, Sherer, Frensch, and Stähler, United States Patent No. 3,157,571 (Nov. 17, 1964)[2]. The importance of molecular dimensions in the case of the herbicidal activities of certain anilides has been reported by Huffman and Allen (1960). The type and position of substituent groups among the salicylic anilides have been shown by Schraufstätter (1962) to have a marked effect on their toxicity to molluscs. Either size or structure or some combination of these or other properties of the molecule may be responsible for the selectively toxic action of the mononitrophenols containing halogens upon lampreys.

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[2] All of these patents are related, directly or indirectly, to the subject matter discussed in this report.

Knowledge of the precise effect of these compounds on lampreys and fishes is still incomplete. Both gross and microscopic pathological examinations of test lampreys and fishes exposed to 3-trifluormethyl-4-nitrophenol and observations of many thousands of specimens from the beginning of exposure to the chemical until their death indicate strongly that they die of a complex of circulatory and respiratory failures (Applegate *et al.*, 1961; Christie and Battle, 1963, Sawyer, 1959). Test lampreys exhibited first an excoriation of the respiratory epithelium with subsequent edema, hemorrhaging, and excessive mucus secretion in the gill pouches. Severe vasodilatation then followed (presumably due to an increase in the permeability of the vascular endothelium and/or relaxation of the vascular nerves) with much of the animal's blood volume accumulating in the now flacid post-cardinal veins and in the hepatic sinuses. Vasodilation by 3-trifluormethyl-4-nitrophenol is consistent with the facts that a nitro functional group is present and that nitrites have been found to be vasodilators (DiPalma, 1964). Agris (1966) found no significant evidence of anoxia in lampreys exposed to the compound but the pathological symptoms observed infer that it must contribute to their death, at least in their final moments of life.

Rainbow trout (*Salmo gairdneri*) exposed to high concentrations of 3-trifluormethyl-4-nitrophenol exhibited the classic symptoms of anoxia in fishes up to the time of their death. Although edema of the gill lamellae and the coating of these with excessive amounts of mucus were evident, no hemorrhaging from the respiratory epithelium took place. Vasodilatation in the trout is apparently restricted to the gills; it was not evident elsewhere in the circulatory system. Christie and Battle (1963) postulate that 3-trifluormethyl-4-nitrophenol enters the body via the gills and that the differential susceptibility of the two species could be attributable to a greater permeability of the respiratory epithelium to the chemical in the larval lampreys than in the rainbow trout as well as to a more generalized toxic effect on the endothelium throughout the lamprey's whole vascular system.

In view of the severity of these symptoms, as observed by ourselves and others, we consider it very possible that the lampreys die simply of acute hypotension (with concomitant circulatory and cardiac failure) and that the death of the trout results directly from an anoxia induced by a progressive mechanical interference with respiration from the accumulation of mucus on the gill epithelium.

Other more subtle pathological conditions of a metabolic nature may also exist and contribute to both the general and selectively toxic properties of various mononitrophenols containing halogens described in this report. The mononitrophenols are known to be methemoglobin-formers (Patty, 1962). Agris (1966), however, found no visual evidence in lampreys killed by 3-trifluormethyl-4-nitrophenol of the brown-colored blood that accompanies the production of methemoglobin. An irreversible block of the uptake of oxygen and inhibition of certain enzymes involved in respiration and carbohydrate metabolism may take place as with the molluscicide BAYLUSCIDE which is also a substituted nitrophenol as well as a salicylanilide[3]. It is also possible to speculate that 3-trifluormethyl-4-nitrophenol and its selectively toxic relatives, like 2,4-dinitrophenol and its related compounds, uncouple oxidative phosphorylation thus causing an increase in oxygen consumption and elevation of the basal metabolic rate (Harborne, 1964). In addition to the metabolic changes possible with exposure to nitrophenols, rates of biological degradation (metabolization) of aromatic structures may vary not only among different species of aquatic vertebrates but also with the nature and location of the substituent atoms or groups in a compound to which a single species is exposed. Maickel, Jondorf, and Brodie (1958; 1959), however, reported that ''fish'' are essentially unable to conjugate ''foreign phenols.'' Maickel (personal communications) reported further that lampreys, like fishes, did not metabolize either certain drugs or phenolic compounds to which they were exposed. He noted, in fact, that the lampreys excreted in an unmetabolized form approximately 95 percent of the phenols taken up by the specimens from the surrounding treated medium.

We attempt in this report to integrate the results of the several diverse series of bioassays, conducted between 1953 and 1961, in which phenols and their related compounds or derivatives were tested to determine if a differential toxic action existed between lampreys and fishes. The results of some of these tests have already been published (*loc. cit.*) but it would be worthwhile at this juncture to summarize briefly the series of testing programs that took place in the order in which they evolved. A total of 4,346 chemicals, predominantly organic compounds, were subjected to rough screening as described by Applegate, Howell, Hall, and Smith (1957). Among all of these test compounds, one chemical, 3-bromo-4-nitrophenol, was found to have the desired biological effect as well as seemingly acceptable physical properties (Fig. 1B). This finding led to a more exhaustive series of tests in which a number of related mononitrophenols containing halogens were examined at closer intervals of concentration and over a wider range of concentrations. The results of these tests, as reported by Applegate *et al.* (1958) and by Applegate *et al.* (1961), brought to 10 the number of compounds that were significantly more toxic to larval lampreys than they were to certain native fishes. The present report increases this list of presumably useful larvicides by five additional substances. Finally, a number of other substituted phenols not tested in the initial screening program, nor in the subsequent "intensive test series" were examined. The results observed for the additional five selectively toxic agents as well as the other substituted phenols just mentioned have not been published or reported upon before. The fundamental purpose of this report is to present the results of all tests, regardless of character, made with the mononitrophenols containing halogens, with the other substituted phenols, and with the phenol derivatives to demonstrate that: (1) Those that are more toxic to lampreys than they are to fishes are associated with a particular molecular structure; and, (2) that very specific differences in the differential toxicities displayed by this group are associated with variations in the structure of this molecule.

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[3] See collected papers in Pflanzenschutz-Nachrichten ''Bayer,'' Vol. 15, No. 1 (1962); published by Farbenfabriken Bayer AG, Leverkusen, West Germany.

Bioassay Methods

Laboratory facilities and equipment were similar to those described by Applegate *et al.* (1957). Bioassay methods for all of the mononitrophenols containing halogens were essentially the same as those described by Applegate and King (1962). Animals were placed in 10-liter glass battery jars (10-inch diameter) each containing 6 liters of test solution. The test jars were aerated by means of standard stone aerators (vigorous aeration does not decrease the concentration of these nonvolatile chemicals). Oxygen levels in the jars during the tests were maintained at near-saturation. Temperatures were held constant at 55° F. by immersion of the test jars in specially constructed water baths.

Test animals were larvae of the sea lamprey (*Petromyzon marinus* L.) and fingerling rainbow trout (*Salmo gairdneri*). Lamprey larvae ranged from 3.5 to 5.0 inches and rainbow trout from 4.5 to 5.5 inches in total length. All larvae were collected from a restricted area of the Ocqueoc River, Presque Isle County, Michigan. The rainbow trout were obtained from a hatchery of the Michigan Department of Conservation. In all experiments with this group of substances, two specimens of larval lampreys and two of rainbow trout were placed in each test container. After the animals were tempered and acclimated to the test temperature, appropriate amounts of a compound in aqueous solutions were added to produce the desired concentrations. All compounds were purchased or synthesized by us as C. P. grade materials. However, when any doubt as to purity existed, *e.g.*, the melting point of a sample was significantly lower than that reported in the literature, the chemical was recrystallized from an appropriate solvent until a suitable substance was produced.

In the initial test of each chemical, two simultaneous replications were made to give a total of four individuals of each species exposed at each concentration up to a maximum of 40 ppm. No further tests were made with those mononitrophenols containing halogens that were biologically inactive at this maximum concentration nor with those that were unquestionably more toxic to rainbow trout than to larval lampreys at any concentration. All compounds in this group that were more toxic to lampreys than to fishes were tested again to determine their biological activity with more precision. Eight to 16 simultaneous replications were run with a total of 16 to 32 individuals of each species at each concentration. In these tests the intervals between concentrations varied from as little as 0.5 ppm to no more than 2 ppm and were so selected that accurate mortality curves could be devised. In the tabular material that is presented subsequently, the concentrations required to kill 100 percent of the larval lampreys and 25 percent of the rainbow trout are given only for those compounds that were more toxic to lampreys than to rainbow trout. The values given were derived from the mortality curves[4].

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[4] Deviations of the LD_{100}/24 hrs. for lampreys and LD_{25}/24 hrs. for rainbow trout between those given in this report and those given in earlier publications are unquestionably due to the time of year when the several investigations were made. Seasonal changes in the biological

Bioassay methods for all other phenolic structures and their derivatives discussed in this report have been described by Applegate *et al.* (1957). The only variation in these methods took place in the rough screening of certain compounds in the period 1957–1960 when either fingerling brook trout (*Salvelinus fontinalis*) or fingerling brown trout (*Salmo trutta*) were substituted as test animals for the rainbow trout when the latter were not immediately available from hatcheries.

Dilution water used in all tests was taken from Hammond Bay of Lake Huron. During the period of years when the tests discussed in this report were conducted, the quality of this water obviously varied from season to season and from year to year. Our records show, however, that the physical and chemical characteristics of the water were usually within the following ranges: Oxygen, 8.5–13.7 ppm; carbon dioxide, 0.5–9.0 ppm; methyl-orange alkalinity, 90–118 ppm; phenolphthalein alkalinity, 0.0 ppm; pH, 7.5–8.2; and, conductivity, 176.3–182.3 micromhos/18°C.

Our tabular material for the phenolics and their derivatives, other than the mononitrophenols containing halogens, give only brief verbal descriptions of the biological activity of the compounds rather than specific concentrations at which they were toxic or nontoxic. We believe that this procedure is necessary because of the variety of test fishes used, variations in water quality over the many years when the tests were conducted, and because most, if not all, of these chemicals were tested at concentrations no higher than 5 ppm. We wish to make it very clear that, with other dilution waters, other test fishes, or at higher concentrations, these compounds might display substantial differences in toxicity other than those that we observed.

Relation of Molecular Structure to Biological Activity

The group of compounds that have the desired selectively toxic properties is a small class of closely related chemicals. These compounds are phenols containing (1) a single nitro group in the 4- position, and, (2) halogens or a trifluormethyl group substituted directly on the ring (Fig. 1C). The trifluormethyl group is more effective than halogen atoms. Among the halogens,

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activity of the halo-mononitrophenols have been reported by Applegate *et al.* (1961). Another study that may have some bearing on this phenomenon is that by Ivanova-Berg and Sokolova (1959).

bromine and chlorine are somewhat more effective than fluorine. The most desirable substances from a practical standpoint are those having a single halogen or trifluormethyl group in the 3-position.

Table 1 summarizes the data for 31 mononitrophenols containing either halogens or a trifluormethyl group. Thirteen of these compounds are derived from 4-nitrophenol and 17 are derived from 2-nitrophenol. Numerous attempts were made to secure compounds related to 3-nitrophenol but only one such compound was obtained. Many of the halogenated 3-nitrophenols are reported in the literature but facilities for preparing them were not available. Except for iodine, all of the halogens and trifluormethyl are well represented[5].

All of the trifluormethyl, monohalogen, and dihalogen derivatives of 4-nitrophenol studied were significantly more toxic to lamprey larvae than to fishes. This was not the case with the tri- and the tetra-halogen-4-nitrophenols tested. These were much more toxic to fish than to lamprey larvae. Furthermore, these compounds killed fish at much lower concentrations than did any of the mono- or disubstituted 4-nitrophenols. It appears that the addition of more than two halogen atoms results in an ''overloading'' of the molecule with such a pronounced increase in the toxic effect upon fishes that the compounds become more toxic to these than to lampreys. This is not the first time this effect has been observed. Schraufstätter (1962), commenting on the moluscicidal activity of chloronitroanilides of salicylic acid, observed the same thing in polychloro derivatives.

Among the monosubstituted derivatives of 4-nitrophenol, the monofluorine derivatives are the least toxic and show a narrower differential toxicity than other members of this group. There is little difference between the chlorine and the bromine derivatives. They are significantly more toxic than the fluorine compounds and show a more pronounced differential toxicity. There is no consistent change in toxicity among any of the pairs of halogen-4-nitrophenols when the halogen is moved from the 2- to the 3- position.

The two trifluormethyl-4-nitrophenols differ from the fluorine, chlorine, and bromine compounds discussed previously. First, there is a marked difference in effect associated with the position of the trifluormethyl group. When this group is in the

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[5] No great effort to obtain the iodonitrophenols was made since these compounds are notoriously unstable and presumably would not have been suitable for either critical bioassays or practical application.

Table 1. Toxic effects of 31 mononitrophenols containing halogens or a trifluormethyl group on larval lampreys and fingerling rainbow trout.

[All tests conducted for a 24-hour period at a water temperature of 55°F.
No tests of compounds conducted at concentrations greater than 40 ppm.
Abbreviations: Lampreys = larval lampreys; RBT = rainbow trout]

Compounds	Biological activity				Properties of compounds selectively toxic to lampreys		
	No toxic effect on either lampreys or RBT	Equally toxic to lampreys and RBT	More toxic to RBT than to lampreys	More toxic to lampreys than to RBT	LD_{100}/24 hrs. for lampreys (ppm)	LD_{25}/24 hrs. for RBT (ppm)	Differential toxicity expressed as ratio of concentrations
Derived from 2-nitrophenol:							
3-fluoro-			X		-	-	-
4-fluoro-	X				-	-	-
5-fluoro-	X				-	-	-
6-fluoro-	X				-	-	-
4,5-difluoro-			X		-	-	-
4,6-difluoro-			X		-	-	-
3-chloro-			X		-	-	-
4-chloro-			X		-	-	-
5-chloro-				X	3	5	1.7
4,5-dichloro-			X		-	-	-
4,6-dichloro-			X		-	-	-
3,4,6-trichloro-				X	5	17	3.4
4-bromo-			X		-	-	-
5-bromo-		X			-	-	-
4,6-dibromo-			X		-	-	-
3-trifluormethyl-				X	<15	>40	2.7^{+}
4-trifluormethyl-			X		-	-	-

Table 1 (Continued).

Derived from 3-nitrophenol:					
2-iodo-		X	>3	4	1.0^+
Derived from 4-nitrophenol:					
2-fluoro-		X	17	23	1.4
3-fluoro-		X	12	17	1.4
2-chloro-		X	7	12	1.7
3-chloro-		X	4	10	2.5
2,5-dichloro-		X	3	13	4.3
2,6-dichloro-		X	?†	?†	?†
2,3,6-trichloro-	X		–	–	–
2,3,5,6-tetrachloro-	X		–	–	–
2-bromo-		X	5	12	2.4
3-bromo-		X	5	11	2.2
2,6-dibromo-		X	19	25	1.3
2-trifluormethyl-		X	13	19	1.5
3-trifluormethyl-		X	2	9	4.5

[†] Tolerances poorly defined due to low solubility of compound.

2- position, the compound is intermediate between the fluoro and the chloro analogues, both in general toxicity and differential toxicity between lampreys and fishes. When the trifluormethyl group is in the 3- position, however, the LD_{100} for lampreys drops to 2 ppm and the differential toxicity rises to 4.5 (see Table 1). This combination of properties is responsible for the widespread use of 3-trifluormethyl-4-nitrophenol (TFM) in sea lamprey control (Applegate *et al.*, 1961; Great Lakes Fishery Commission, 1961, 1962, 1963, 1964).

Of the 17 substituted 2-nitrophenols, three are selectively toxic to lampreys, ten are selectively toxic to fish, and three are biologically inactive. One compound is equally toxic to both fish and lampreys. Any close comparison of the monosubstituted 2-nitrophenols with similar 4-nitrophenols is out of the question. In both cases, the nitro group is in a position to enhance the acidity of the phenolic group by means of resonance interaction with the benzene ring (Figs. 1D and 1E)[6]. On the other hand, only in the 2-nitrophenols is there a strong intramolecular hydrogen bonding between the nitro and the hydroxyl groups (Fig. 1F). The 4- and 5- substituted derivatives of 2-nitrophenols invite comparison with both 2- and 3- substituted 4-nitrophenols for they all are 1,2,4-trisubstituted benzenes. It is clear enough, however, that the derivatives of 2-nitrophenol are generally less toxic and less selective than those of 4-nitrophenol.

In no instance did any phenol that varied from a structure containing one nitro group and one or more halogens possess any indication of the desired selective toxicity (Tables 2 and 3). Phenol itself was more toxic to fish than to larval lampreys. Twenty of 22 mono-halo-, poly-halo-, and mixed poly-halophenols were similar in this regard; pentachlorophenol was equally toxic to all test animals and pentabromophenol had no toxic effect on any species (Applegate *et al.*, 1957). The three

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[6] In his study of nitrohaloanilides of salicylic acid, Schraufstätter observed that *p*-nitroanilides were more toxic and more selective. A similar but less striking toxic effect was present in the *o*-nitroanilides. However, nitro groups in the meta position did not have this effect. The *m*-nitroanilides were actually less toxic than when the nitro group was absent. It is tempting to speculate that this behavior of the nitro group in the 3- position is associated with its inability to transmit a resonance effect to the amido nitrogen. The only halogenated 3-nitrophenol tested was 2-iodo-3-nitrophenol. It proved to be quite toxic, the lampreys being slightly more susceptible than the fish. The inadvisability of comparing the toxicity of this single substance with that of the other substances is obvious, particularly when it is noted that there are no other iodo compounds with which to compare it.

Table 2. Synopsis of the biological activity among lampreys and fishes characterizing certain phenolic groups.

[Biological activity described in more detail in Table 3.]

Phenol	More toxic to certain fish species than to lampreys (1 compound tested).
Mono- and poly-halo-phenols	More toxic to fish than to lampreys or toxic to fish and not toxic to lampreys except pentachlorophenol which was equally toxic to all species and pentabromophenol which had no toxic effect on any species, at least at 5 ppm (20 compounds tested).
Mixed poly-halo-phenols	Toxic to fish; not toxic to lampreys (2 compounds tested).
Mononitrophenols	No toxic effect on any test species (4 compounds tested).
Dinitrophenols	No toxic effect on any test species (1 compound tested).
Halo-dinitrophenols	No toxic effect on any species except 2-chloro-4,6-dinitrophenol which was toxic to fish but not to lampreys (6 compounds tested).
Halo-trinitrophenols	No toxic effect on any species (1 compound tested).
Poly-halo-mononitrophenols	More toxic to fish than to lampreys (1 compound tested).

mononitrophenols and 2,4-dinitrophenol were biologically inactive at a concentration of 5 ppm. Six of the seven mono-halo-di- and trinitrophenols subjected to the same screening tests were inactive; the exception was 2-chloro-4,6-dinitrophenol which was toxic to fish but not to lampreys. The only mixed halonitrophenol examined was 4-bromo-2-chloro-6-nitrophenol; it was more toxic to fish than larval lampreys[7].

In view of the widespread occurrence of oxidation-reduction processes in living systems, it would have been interesting to

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[7] The biological activity of 24 of these phenolic compounds have been reported by Applegate *et al.* (1957). The toxicity of 12 additional compounds of this type has been determined since this report was issued.

Table 3. Biological activity of phenol and some substituted pheonlic compounds other than mononitrophenols containing halogens.

[“Report No.” refers to numerical designation of compound in Table 1 in report by Applegate *et al.* (1957); “FWS No.” is Accession number of compounds tested, but not yet reported or published anywhere†. Where both “Report No.” and “FWS No.” are given for a chemical, it indicates that early tests with the compound were reported (*op. cit.*), while results of later tests with other samples of the same substance have not been published until now. (Maximum concentration tested, 5 ppm, except where otherwise noted after name of chemical. Abbreviations: RBT = rainbow trout; BrT = brook trout; BT = brown trout; BG = bluegills; and L = larval lampreys].

Report or Accession number	Compound	Biological activity
	Phenol	
Report No. 2704	Phenol (liquified USP XIV)	Toxic to RBT; not toxic to BG & L
	Mono-and poly-halo-phenols	
Report No. 2761	2-chlorophenol	Toxic to RBT; not toxic to BG & L
Report No. 2762	3-chlorophenol	Toxic to RBT & BG; not toxic to L
Report No. 2763	4-chlorophenol	More toxic to RBT & BG than to L
Report No. 2801	2, 4-dichlorophenol	More toxic to RBT than to BG & L
FWS No. 5072; 5230	2, 5-dichlorophenol	More toxic to RBT & BG than to L
Report No. 2605	2, 6-dichlorophenol	ditto
Report No. 2803; FWS No. 5228	3, 4-dichlorophenol	ditto
Report No. 2878	2, 4, 5-trichlorophenol	ditto
Report No. 2879	2, 4, 6-trichlorophenol	ditto
Report No. 2871	2, 3, 4, 6-tetrachlorophenol	ditto
Report No. 2872	2, 3, 5, 6-tetrachlorophenol	ditto
Report No. 2857	pentachlorophenol	Equally toxic to RBT, BG & L
FWS No. 5074	3-bromophenol	More toxic to RBT than to L
FWS No. 5087	4-bromophenol	ditto
Report No. 2790	2, 4-dibromophenol	Toxic to RBT & BG; not toxic to L
FWS No. 5139	2, 4, 6-tribromophenol	More toxic to RBT & BG than to L
Report No. 2856	pentabromophenol	No toxic effect on any species
FWS No. 5146	2-iodophenol	More toxic to RBT than to L
Report No. 2829	4-iodophenol	Toxic to RBT & BG; not toxic to L
FWS No. 5145	2, 4, 6-triiodophenol	More toxic to RBT & BG than to L

Table 3 (Continued)

	Mixed poly-halo-phenols	
Report No. 2721	4-bromo-2, 6-dichlorophenol	Toxic to RBT & BG; not toxic to L
Report No. 2792	2, 6-dibromo-4-chlorophenol	ditto
	Mononitrophenols	
Report No. 2844	x-nitrophenol	No toxic effect on any species
Report No. 2845	2-nitrophenol	ditto
FWS No. 5149	3-nitrophenol	ditto
Report No. 2846	4-nitrophenol	ditto
	Dinitrophenols	
Report No. 2814	2, 4-dinitrophenol	Not toxic to L
	Halo-dinitrophenols	
FWS No. 5265	4-fluoro-2, 6-dinitrophenol (40 ppm)	Not toxic to RBT & L
Report No. 2767; FWS No. 5088	4-chloro-2, 6-dinitrophenol (40 ppm)	ditto
Report No. 2766	2-chloro-4, 6-dinitrophenol	Toxic to RBT & BG; not toxic to L
FWS No. 5235	2, 5-dichloro-4, 6-dinitrophenol	Not toxic to RBT, BG, or L
FWS No. 5241	3-bromo-2, 4-dinitrophenol	Not toxic to RBT or L
FWS No. 5239	3-bromo-4, 6-dinitrophenol	ditto
	Halo-trinitrophenols	
FWS No. 5240	3-bromo-2, 4, 6-trinitrophenol	Not toxic to RBT or L
	Poly-halo-mononitrophenols	
FWS No. 5227	4-bromo-2-chloro-6-nitrophenol	More toxic to RBT & BrT than to L

†Test records on file at U.S. Bureau of Commercial Fisheries, Hammond Bay Biological Station, Millersburg, Michigan, 49759.

discover the biological activity of oxidation or reduction products of the selectively active 4-nitrophenols. Unfortunately, the original screening program included few such compounds. The polyhydric phenols such as catechol might be considered as oxidation products. None of the nitro-halo derivatives of these compounds was tested. The three halogenated resorcinols tested were either indiscriminately toxic or more toxic to fish. A second class of oxidation products would be the quinones. No benzoquinones were tested (quinhydrone was biologically inactive). Derivatives of 1,4- and 1,2-napthoquinone, however, were very active biologically, particularly when halogens were present, but were generally more toxic to fish than to larval lampreys. Further examination of this class might prove to be interesting.

In considering reduction products of the nitrophenols, a chemist would first think of azo and azoxy benzenes. Seven compounds which belonged to this class were tested, but none was toxic at 5 ppm except for two instances when a phenolic and a nitro group were also present [2-nitro-4-phenylazophenol and 4-(4-nitrophenylazo)phenol]. These two compounds were more toxic to fish than to larval lampreys.

The end reduction product of a nitro group is an amino group. No phenols containing halogen and an amino group were tested. The unsubstituted aminophenols are inactive. In this behavior, they resemble the mononitrophenols although 4-aminophenol exhibited indiscriminate toxicity. Anilines can be considered as nitrogen analogues of phenols rather than reduction products of aromatic nitro compounds. Anilines and nitroanilines are generally nontoxic unless a halogen is present. When a halogen, with or without a nitro group, is present, the compounds are either equally toxic to lampreys and fishes or they are more toxic to fish.

The original screening program included also a wide variety of compounds related to phenol that might be expected to have biological properties similar to the halo-nitrophenols. Most of these chemicals were alkylated phenols like the cresols but a fair number of naphthols were also included. When these compounds contained neither halogen nor nitro groups, they exhibited no biological activity. A single nitro group did not make these related compounds toxic, but two nitro groups did. Seven dinitro-alkylphenols (*e.g.*, 4,6-dinitro-2-cresol) were tested; all of them were toxic but none was significantly more toxic to lampreys than to fish. A single halogen atom often sufficed to produce a toxic substance (*e.g.*, 6-bromo-2-naphthol) and additional halogens usually intensified the effect, but among more than 30 mono- and polyhalogenated substances, none was more toxic to lamprey larvae than to fish. Eight alkylated phenols containing halogen and nitro groups were examined (*e.g.*, 4-bromo-6-nitro-2-cresol) but all of them were either indiscriminately toxic or more toxic to the fish.

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Species Difference in the Composition of Milk with Special Reference to the Northern Fur Seal[1]

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Abstract

Gross composition is given for five samples of milk from the northern fur seal (*Callorhinus ursinus*). The major component was fat (43% of the whole milk). Fatty acid distribution by gas chromatography showed more long-chain fatty acids were unsaturated chains in the range of 20–22 carbons) than any other species studied: cow, water buffalo, goat, and sow. Fur seals' milk fat had no fatty acid with chain length less than 10 C. Reducing sugars amounted to less than 0.1%. Casein accounted for about 50% of the total nitrogen. The major casein fraction appears to be β-casein. The major ash constituents were the same as those found in cows' milk, but the total amounts were less.

Considerable interest is being shown in the comparative evolutionary and genetic trends in milk composition. Of a particular milk, it can be assumed that the composition has evolved to meet the nutritional requirements of that species. Usually, variations in milk composition are relatively slight among individuals within a species, but considerable among females of different species.

A review of the results published before 1959 from species not normally used as a source of milk for human consumption has been prepared by Evans (7). Some of the older work may have limited accuracy, because of the crude methods of analysis then available. Most data reported have been scanty. Often the animal was dead before the sample was secured.

Several recent conributions have come to the attention of the authors (2–4, 7). Of special interest to this study was the work of Pilson and Kelley (15) on the composition of the milk of the California sea lion. In a sample containing 52.7% total solids, he found 36.5% fat, 13.8% protein, and no lactose, as shown by paper chromatography. The main protein fraction was casein, which had a lower phosphorus content than bovine casein and an apparently higher pH for maximum flocculation.

One approach to the nutritional requirements for growing animals lies in a study of the composition of the milk they receive during the suckling period. The present study was undertaken to establish a sound basis for the preparation of an artificial milk for pups of the northern fur seal (*Callorhinus ursinus*). Such a diet would make possible the study of these pups in captivitiy, their physiology and pathology. A good description of the northern fur seal has been given (5).

Collection of the samples. Milks for these analyses were collected from live seals caught with a lariat on St. Paul Island, Alaska, as they came ashore to nurse their pups. Nursing females are away, feeding, an average of eight days between one- to two-day nursing periods. Pups are weaned at about four months of age (5).

The females were tranquilized by the intramuscular injection of 200 mg propriopromazine and strapped to a portable wooden platform. The surface of the platform was partially cut away to provide access to the mammary glands, diffusely spread over the lower abdomen. There are two abdominal and two inguinal glands. Nipples are retractile and difficult to grasp. Milk let-down was effected by intravenous injection of 40 U.S.P. units of oxytocin. Either the superficial volar carpa vein of a foreflipper or interdigital vein of a hindflipper was used. A sample of 170 ml could be obtained from a 45-kg female. Half of each sample was pasteurized and the other half preserved as 0.5% phenol. All samples were promptly shipped by air to the laboratory.

Methods of Analysis

Total solids were determined by drying at 100 C to constant weight in vicor dishes. Ash was determined on the same samples after 4 hr in a muffle furnace at 600 C. The ash was dissolved in dilute HCl for mineral analyses. Fat determinations were by the Mojonnier method. Extra amounts of fat for fractionation were

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prepared by acetone extraction of the whole milk. The method of Smith (16) was used for preparation of methyl esters of the fatty acids. For the gas-liquid chromatographic separation of the fatty acids, a Barber-Colman Model 15C, equipped with a hydrogen flame detector, was used. The 6-ft glass column was packed with 20% diethylene glycol succinate (DEGS) on chromosorb W 45/60 mesh. Nitrogen was the carrier gas.

Thin-layer chromatography was performed on silica gel G containing $CaSO_4$ as a binder, using the Camag apparatus. The solvent system was petroleum ether, diethyl ether, and acetic acid (80:20:1) according to the procedure of Wood (17).

Reducing sugars were determined by the picric acid method of Perry and Doan (11). No attempt was made to identify the small amount of reducing material present.

Proteins were determined by the Kjeldahl method (N × 6.38). Difficulty was encountered in the isoelectric precipitation of casein in the presence of the fat. Consequently, we resorted to a preliminary extraction in the cold wtih 10 vol acetone. The dried residue was then used for nitrogen distribution studies with the method of Aschaffenburg and Drewry (1). Some nonprotein-nitrogen may have been removed by the acetone extraction.

Amino acid analyses were performed in the Department of Agricultural Chemistry. Cystine was protected by first converting to cysteic acid with performic acid. The amino acid analyzer equipment manufactured by Technicon Chromatographic Corporation was used. The procedure was a modification of that prepared by Piez and Morris (14).

Results and Discussion

Gross composition. Milk of the northern fur seal has the texture of thick cream. It is white in color, with sometimes a slight tinge of gray, and has a distinctly fishy odor. Table 1 shows the composition of five samples collected over a 3 yr period. During 1965 three samples were analyzed as shown. The first represented colostrum, since it was collected within 4 hr of parturition. Samples collected on August 29 and October 24, 1965, represent mid- and late lactation, respectively. All samples were from different females. Data in the table show that milk of the fur seal is very high in total solids, which agrees with data on other species of animals normally inhabiting the ocean, Evans (7). The major component is fat which averages over 50% of the total weight. Nonfat solids are mainly protein. Of great interest to comparative biologists is the presence of only trace amounts of reducing sugars. Similar observations were made by Pilson (15) for the California sea lion. Apparently the young of these species do not require lactose in their diet. The ash content of these samples averaged about 0.5%, low compared with most mammals. Pilson and Kelley (15) give a value of 0.64% ash in one sample of sea lion milk. The pH of the fresh seals' milk falls below that of cows's milk, 6.4–6.8. The milk of the fur seal collected on the first day post-partum showed no great difference in composition from those samples collected during mid-lactation.

Composition of the fat. Use of gas-liquid chromatography has greatly simplified the analysis of component fatty acids. For comparative purposes the milk fatty acids from seven species are shown in Table 2. Using identical technique we have analyzed the milk fat from three species of ruminants (cow, Indian water buffalo, and goat) and two species of nonruminants (fur seal, pig). Two additional comparisons were taken from the literature. The most striking differences between the milk fat of ruminants and nonruminants lie in the values for short-chain acids. Fatty acids, shorter than 14-carbon atoms, comprise

TABLE 1
Gross composition of fur seals' milk

	Date of collection				
	August 1963	August 1964	July 1965	August 1965	October 1965
	(%)				
Total solids	63.6	53.8	71.1	65.6	72.3
Fat	51.1	43.0	58.2	54.2	59.8
Nonfat solids (by difference)	12.5	10.8	12.4	11.4	11.9
Protein	11.3	10.2	8.7	9.2	8.4
Reducing sugars (unidentified)	0.07	0.08	0.14	0.14	0.13
Ash	0.49	0.52	0.40	0.56	0.55
pH	5.9	5.8	6.4	6.0	6.4
Calcium and magnesium, (*mg %*)			32.	80.	60.
Phosphorus (*mg %*)			51.	53.	48.
Chlorine (*mg %*)			.. ..	124	....

TABLE 2
Major fatty acid components of milk fat from different species—ruminants and nonruminants

Symbol	Cow	Indian water buffalo	Goat	Fur seal	Sow	Human [a]	Mare [b]
	(% by wt)						
4:0	1.4	0.6	1.3	0.0	0.0	0.4	0.4
6:0	2.3	2.0	2.1	0.0	0.0	0.1	0.9
8:0	1.6	1.0	3.7	0.0	0.1	0.3	2.6
10:0	3.8	2.1	11.1	0.4	0.2	2.2	5.5
10:1	0.6	0.2	0.4	0.0	0.0	0.1	0.9
12:0	5.1	2.9	4.8	0.2	0.4	5.5	5.6
12:1	0.0	0.0	0.0	0.0	0.0	0.1	0.1
13:0	0.4	0.0	0.2	0.0	0.0	0.0	0.0
14:0	9.5	9.5	12.6	6.5	6.0	8.5	7.0
14:1	4.8	4.8	2.3	1.1	0.6	0.6	1.8
15:0	0.9	0.7	0.5	0.0	0.0	0.0	0.0
16:0	15.9	16.7	27.5	16.0	17.6	23.2	16.1
16:1	7.4	6.5	2.6	9.4	11.9	3.0	7.5
17:0	0.0	0.0	1.4	1.3	0.0	0.0	0.0
18:0	16.6	17.9	8.5	2.4	11.6	6.9	2.9
18:1	23.9	26.1	18.9	26.7	29.0	0.0	0.0
18:2	4.5	3.3	1.4	3.8	19.2	0.0	0.0
18:3	1.4	3.5	0.0	17.4	3.9	0.0	0.0
20:0	0.0	0.0	0.6	0.0	0.0	1.1	0.3
20:1	0.0	0.9	0.0	4.1	0.0	0.0	0.0
22:0	0.0	0.0	0.0	0.0	0.0	7.8	4.2
22:1	0.0	1.4	0.0	5.4	0.0	0.0	0.0
22:2	0.0	0.0	0.0	5.2	0.0	0.0	0.0

[a] Baldwin and Longenecker (6).
[b] Hilditch and Jasperson (10).

only 0.6% of the total in fur seal milk, but 15 and 23% in milk of the cow and goat, respectively. On the other hand, fur seals' milk showed a higher percentage of fatty acids with a chain length of more than 20 carbons 14.7% of total fatty acids). The dietary intake of the different species helps to determine the fatty acid composition of the milk fat. Short-chain fatty acids probably are contributed by rumen microflora.

Fur seal milk fat is highly unsaturated, as may be seen from Table 2. Over 70% of the total component fatty acids had one or more double bonds. Others have reported a high degree of unsaturation in seal milk fat (7).

Thin-layer chromatography was used to identify major fat components. Figure 1 shows the comparison of fur seal milk fat with various reference compounds. Most significant was the large spot having the same Rf value as tripalmitin. Milk fat from other species run at the same time (Figure 2) show more spreading of the triglyceride spot. There is evidence in all species for the presence of cholesterol and phospholipids, the latter remaining at the origin in the solvent mixture used. Fur seal milk fat differed from the other species in showing a larger spot at the origin after elution in the mixed solvents. A striking observation was the appearance of a purple color immediately upon heating, after spraying the spots with 50% sulfuric acid. Fur seal milk fat phospholipid spots were the only ones showing this color change.

Analysis of the phospholipid fraction showed no fatty acids with less than 14 carbons. Milk fat phospholipids from the cow and goat showed 8:0, 10:0, and 12:0 fractions when analyzed under the same conditions.

Composition of the protein fraction. The major protein component of the milk of most species is casein. Normal cows' milk contains

TABLE 3
Distribution of nitrogen in the milk of fur seal expressed as per cent of total nitrogen

Collection date	August 1964	July 1965	August 1965	October 1965
Casein	55.3	44.0	50.7	52.0
Albumin and globulin	22.0	33.0	22.0	21.0
β-Lactoglobulin	......	25.0	......	28.0
Proteose-peptone	19.3	20.9	......	......
Nonprotein nitrogen	......	......	7.0	......

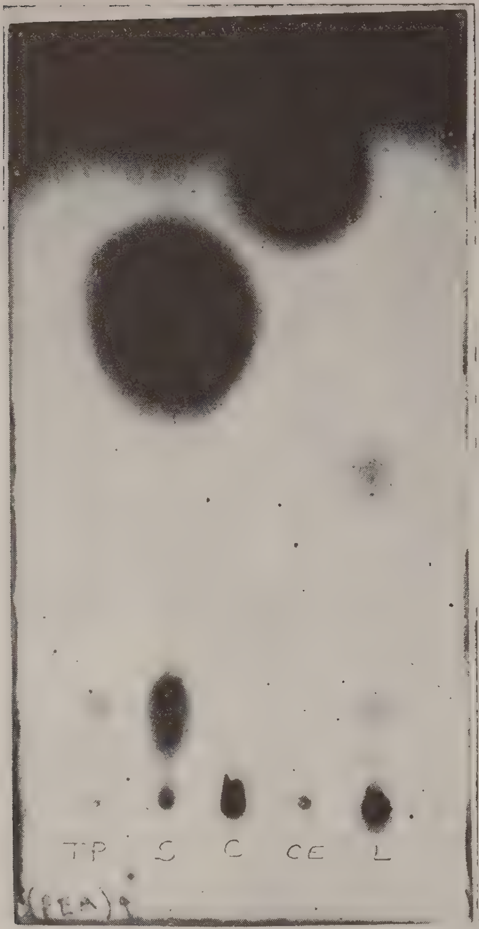

FIG. 1. Photograph of a thin-layer chromatogram showing the separation of fur seal milk fat (S) compared with that of reference compounds: tripalmitin (TP), cephalin (C), cholesterol ester (CE), and lecithin (L).

75–80% whole casein. Milk of the fur seal, as shown in Table 3, has about 50% of the total N in the form of casein. When the noncasein proteins were fractionated by sodium sulfate solutions (1), about 25% of the total nitrogen was found to be β-lactoglobulin. About 20% of the total nitrogen was proteose-peptone, whereas about 7% was nonprotein nitrogen.

Paper electrophoresis (12) of the casein fraction in the presence of 5 M urea showed a major band having the same mobility as β-casein. This might account for the low phosphorus content of sea lions' milk casein, as reported by Pilson and Kelley (15).

TABLE 4
Amino acid content of fur seal milk proteins compared with casein from cows' milk

Amino	Fur seal milk	Bovine casein[a]
	(%)	
Aspartic Acid	6.6	7.1
Threonine	3.5	4.9
Serine	2.4	6.3
Glutamic Acid	16.9	22.4
Proline	8.1	11.3
Glycine	1.3	2.7
Alanine	3.9	3.0
Cystine	0.11	0.34
Valine	5.9	7.2
Tryptophane	Not determined	1.7
Isoleucine	4.2	6.1
Leucine	8.9	9.2
Tyrosine	3.9	6.3
Phenylalanine	3.7	5.0
Lysine	5.0	8.2
Histidine	2.4	3.1
Arginine	4.2	4.1
Cysteic acid (as cystine)	1.67	....
Methionine sulfone (as methionine)	2.08	2.8
Total	82.7	111.7

[a] Jenness and Patton (11).

The amino acid content of seals' milk proteins (Table 4) was found to be similar to that reported for bovine casein (11), except for somewhat lower amounts of dicarboxylic acids (glutamic and aspartic). The lower content of dicarboxylic acids may account for the slower paper electrophoretic mobility in veronal buffer (pH 8.6 containing 5 M urea), of the major protein fraction of fur seals' casein compared to bovine casein.

Ash analysis. Low values for ash, shown in Table 1, no doubt reflect the high content of fat in fur seals' milk, although the nonfat solids also are higher than cows' milk. Calcium plus magnesium titrated together with versene gave values about half the average value given for cows' milk (11). Phosphorus likewise amounted to about 50% of the normal values reported for cows' milk. Chloride, determined in one sample by the method of Herrington and Kleyn (9), gave a value of 124 mg chlorine per 100 g whole fur seals' milk. This is above that reported as the average value (100 mg) for cows' milk (11).

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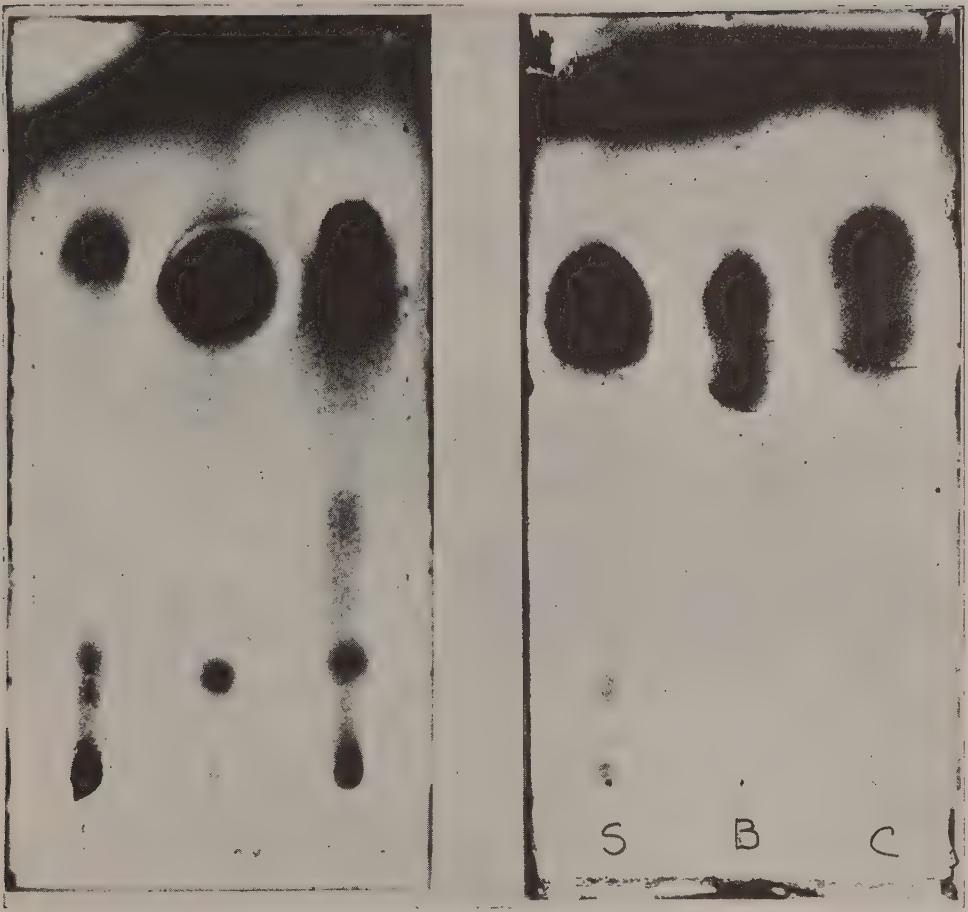

FIG. 2. Photograph of a thin-layer chromatogram showing the comparison of the lipid fractions of the different species. From left to right: seal, sow, goat, seal, buffalo, cow. The spots represent, beginning at origin (bottom of plates): phospholipids, cholesterol, free fatty acids, triglycerides.

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ABSORPTION OF FLUID FROM ISOLATED INTESTINE OF THE TOADFISH, *OPSANUS TAU*

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Abstract—1. Movement of water from isolated intestinal sacs of toadfish, *Opsanus tau*, was measured by using C^{14}-inulin as a tracer. Changes in Na concentration were followed also.

2. Net water absorption was $25{\cdot}7 \pm 14{\cdot}5$ (S.E.) $\mu l\ hr^{-1}\ g^{-1}$, wet weight, when identical Ringer solutions bathed mucosal and serosal surfaces. Absorption decreased in the presence of 10^{-3} M NaCN and 10^{-3} M NaCN plus 10^{-4} M IAA.†

3. The direction of water movement was reversed and mucosal concentration of Na rose when five-sixths of the mucosal NaCl was replaced by the non-penetrating solute, mannitol. When only one-third of the mucosal NaCl was replaced with mannitol, water absorption continued and mucosal Na fell, but net water flow was reversed in the presence of 10^{-3} or 10^{-4} M IAA plus 10^{-4} M DNP.‡

4. A possible interpretation is that salt and water movements are coupled and that salt transfer can occur against a concentration gradient.

INTRODUCTION

Absorption of water and solutes by the intestine has been studied in several mammalian species (Clarkson & Rothstein, 1960; Curran & Solomon, 1957; Schultz & Zalusky, 1964), but little is known about this process in lower vertebrates. In marine teleosts the role of the intestine in osmoregulation was pointed out by Smith (1930) who showed that marine fish continually ingest sea water and absorb ions and water from the intestine. These activities, coupled with elimination of ions by the gills, contribute to the maintenance of a blood composition hypotonic to sea water.

Recently House & Green (1963, 1965) studied intestinal absorption in the marine fish, *Cottus scorpius*. They found that water was absorbed in the absence of an osmotic gradient and that there was an electrically neutral transport of NaCl. The present investigation deals with intestinal fluid movement in a different marine teleost, the toadfish, *Opsanus tau*.

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† IAA = iodoacetic acid. ‡ DNP = 2,4-dinitrophenol.

MATERIALS AND METHODS

Toadfish were caught in the Beaufort Inlet, North Carolina, and maintained in flowing sea water until used. They were anaesthetized in MS 222* (tricaine methanesulphonate, Sandoz Pharmaceuticals, Hanover, New Jersey) and the intestine removed. Segments about 3 cm long were tied off at one end and suspended as open sacs from a syringe barrel in 250 ml of continuously oxygenated Ringer (composition: 9 g NaCl, 40 ml 0·154 M KCl, 15 ml 0·11 M NaH_2PO_4, 85 ml 0·11 M Na_2HPO_4 to 1 l. with distilled water).

Intestinal sacs were filled with 1–2 ml of Ringer solution containing 1–2 μc of C^{14}-inulin. Net water movements during 5–6 hr were determined by the change in inulin concentration in 20 μl samples removed periodically from the sacs. The intestines were almost impermeable to inulin since, after 5 hr, no more than 2 per cent of the amount present initially was detected in the bathing medium.

The concentration of NaCl in the mucosal Ringer solution was varied by replacement with an osmotically equivalent amount of mannitol. Mannitol was considered effectively non-penetrating, since with C^{14}-mannitol only 3 per cent of the amount present initially was detected in the bath after 5 hr.

C^{14} was measured in a gas-flow detector (Nuclear Chicago, Model C-115) and Na was analyzed on a Beckman DU spectrophotometer with flame attachment.

Experiments were performed at room temperature (20–23°C). Wet weights were obtained at the end of an experiment after the tissue between the ties was removed and blotted. Weights ranged between 1–3 g.

RESULTS AND DISCUSSION

A net movement of water occurred from mucosa to serosa when identical Ringer solutions bathed both sides of the intestinal wall (Table 1, Group A). Water absorption decreased significantly ($P < 0{\cdot}001$) in the presence of 10^{-3} M NaCN or 10^{-3} M NaCN plus 10^{-4} M IAA. Therefore absorption of water took place in the absence of an osmotic gradient and was in some way dependent upon metabolism.

Water absorption persisted when one-fifth or one-third of mucosal NaCl was replaced by mannitol, a non-penetrating solute (Groups B and C). The concentration of mucosal Na decreased, especially in Group C experiments. With metabolic inhibitors (IAA plus NaCN or DNP) the rate of absorption decreased significantly ($0{\cdot}02 < P < 0{\cdot}05$) when the NaCl gradient was 1·2 (Group B), and when the gradient was 1·6 the direction of net water movement was reversed (Group C). Thus water absorption could continue even when concentration gradients of NaCl favored passive entry of salt.

In contrast, the direction of net water flow was from serosa to mucosa when five-sixths of the mucosal NaCl was replaced by mannitol (Group D). This flow was not significantly altered by metabolic inhibition with 10^{-4} M DNP plus 10^{-3} M IAA. The mucosal concentration of Na doubled during these experiments

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* Trade names referred to in this publication do not imply endorsement.

(Group D, first and second columns). The data suggest that Na, accompanied by water, diffused passively down its concentration gradient.

In summary, water absorption across toadfish intestine can occur in the absence of an osmotic gradient and persists, with a decrease in mucosal Na concentration, when there is a serosal to mucosal NaCl gradient of 1·6. Metabolic inhibitors diminish or reverse this absorption and prevent the fall in mucosal Na concentration. When the serosal to mucosal NaCl gradient is as high as 4·8, however, the direction of net water movement is reversed and the mucosal Na concentration increases. The data are consistent with the view that water movement is coupled to salt transfer and that salt transfer is by an active process; additional evidence is necessary to prove this hypothesis.

TABLE 1—WATER AND Na CHANGES IN ISOLATED SACS OF TOADFISH INTESTINE

Group*	Initial mucosal Na (mEq/l)	Final mucosal Na (mEq/l)		Net water flow‡ (μl hr^{-1} g^{-1}, wet weight)	
		Control	Inhibited†	Control	Inhibited†
A	188	171 ± 4 (2)	—	−25·7 ± 14·5 (6)	−5·2 ± 3·7 (4)
B	151	146 ± 1 (2)	147 ± 0 (3)	−40·5 ± 9·6 (4)	−10·4 ± 3·5 (4)
C	115	79 ± 4 (4)	121 ± 5 (4)	−35·7 ± 3·0 (5)	+6·6 ± 7·4 (4)
D	39	70 ± 0 (2)	—	+34·7 ± 5·0 (3)	+81·5 ± 49·6 (2)

Results expressed as mean ± standard error (number of measurements).

* Groups A, B, C, D refer to initial mucosal Na concentration. Serosal Na 182 mEq/l in all cases.

† Group A: 10^{-3} M NaCN or 10^{-3} M NaCN plus 10^{-4} M IAA. Group B: 10^{-3} M NaCN plus 10^{-4} M IAA or 10^{-4} M DNP plus 10^{-4} M IAA. Group C: 10^{-4} M DNP plus 10^{-4} or 10^{-3} M IAA. Group D: 10^{-4} M DNP plus 10^{-3} M IAA.

‡ Absorption from the mucosal surface indicated by a minus sign; net entry of water into lumen shown by a plus sign.

The hypothesis that active transport of salt is the driving force for net water flow agrees with the conclusions of Curran & Solomon (1957) and Clarkson & Rothstein (1960) on rat intestine and with those of Diamond (1962) for fish gall-bladder. In the marine teleost, *Cottus scorpius*, House & Green (1963, 1965) found active transport of NaCl, and water movement in the absence of osmotic gradients which was sensitive to metabolic inhibitors. They calculated that the concentration of NaCl in the fluid moving between identical Ringers was three to four times higher than that of the Ringer. In toadfish intestine there was no evidence for absorption of a greatly hypertonic fluid; in the two experiments for which the necessary data are available, the concentration of Na in the moving fluid was 211 and 232 mEq/l, compared to a Na concentration of 182 in the bathing medium.

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Uptake of Mixed Fission Products by Marine Fishes

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ABSTRACT

Laboratory experiments were conducted to measure uptake of fission products by fish from water and from oral doses. Availability of fission products to the fish was curtailed considerably by the formation and settling of radioactive particles in the water and by sorption to abiotic surfaces. Spot, *Leiostomus xanthurus*, and Atlantic croaker, *Micropogon undulatus*, accumulated relatively low levels of radioactive material from seawater. Following a single oral dose, croaker assimilated a maximum of 14% in 4 hours, but 94% of the original dose was eliminated after 4 days. Bluefish, *Pomatomus saltatrix*, assimilated only 3% of the cumulative dose of mixed fission products administered in shrimp meat on alternate days for 55 days. Of the amount assimilated from oral doses by croaker and bluefish, the largest concentrations were found in the internal organs.

INTRODUCTION

Considerable interest has been centered on investigations of the uptake of radioactive materials by fish and other organisms after the release of these materials into the aquatic environment. Most of the data on uptake of fission products by marine organisms have been obtained from radiological surveys of the environment. An extensive account of the surveys conducted in the Pacific atomic-bomb-testing area by the Radiation Laboratory of the University of Washington has been published by Hines (1962). Other reports on both experimental and field investigations appear in Radioecology (Schultz and Klement, 1963). A major share of the experimental work pertains to the uptake of individual radionuclides, rather than mixtures, by various aquatic organisms. Among the few reports on experimental work with fission product mixtures are those by Gong et al. (1957), who measured the uptake of radionuclides by clams from a 2-month-old mixture of fission products, and by Rice, Baptist, and Price (1964), who conducted experiments on uptake by plankton, shellfish, shrimp, and fish.

To cope with the problem of release of radioactive materials into the aquatic environment, much more experimental work is needed on the uptake of fission products—both mixtures and individual radionuclides. The difficulties which may be encountered in working with the mixtures can readily be understood when one realizes that fission of U-235 in a reactor produces as many as 80 primary fission products, many of which decay into numerous daughter products ranging in mass numbers from 72 to 160 (Glasstone and Sesonske, 1963). The composition of these mixtures changes with time because of the varying physical half-lives of the individual isotopes, which range from a fraction of a second to many years. The purpose of the present investigation was to measure uptake of fission products by fish from seawater and from gastro-intestinal absorption of orally administered fission products.

METHODS

Uptake of fission product mixtures from seawater was studied in spot, *Leiostomus xanthurus* (15 to 32 grams) and Atlantic

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[1] This research was supported through a cooperative agreement between the U. S. Fish and Wildlife Service and the U. S. Atomic Energy Commission.

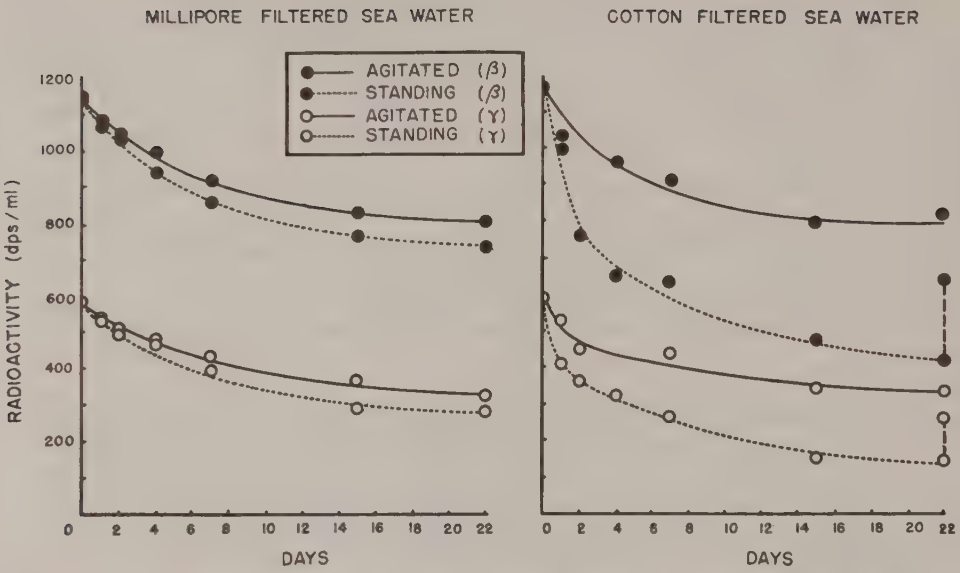

FIGURE 1.—Loss of radioactivity near the surface of Millipore-filtered and cotton-filtered seawater due to formation of particles and surface adsorption of fission products. Cotton-filtered standing water was mechanically agitated for 0.5 hour on the 22nd day (vertical dashed lines).

croaker, *Micropogon undulatus* (66 to 114 grams). Uptake from orally administered doses by croaker and bluefish, *Pomatomus saltatrix* (273 to 574 grams) was also determined. All fish used in these experiments were collected near Beaufort, North Carolina. The experiments were conducted at various times during a 2-year period, so that the fission product mixtures varied considerably in age. The fission products, obtained from the Oak Ridge National Laboratory, were in a 3N nitric acid solution and had decayed less than 45 days when shipped.

Since many fission products are known to be particulate in seawater (Greendale and Ballou, 1954), a test for particle formation was conducted with four 1-liter glass-stoppered Erlenmeyer flasks containing equal amounts of a 248-day-old mixture of fission products in seawater. In order to measure the formation of radioactive particles, it was necessary to first remove particles already present by Millipore-filtering the water in two flasks and cotton-filtering the water in the remaining two flasks. Samples of 1 ml were pipetted from a few millimeters below the surface in each flask and measured for radioactivity. Samples to be measured for beta (β) activity were prepared by drying the sample in a planchet. Those to be measured for gamma (γ) activity were pipetted into vials. Before pipetting each sample, one flask of Millipore-filtered water and one of cotton-filtered water were vigorously agitated for 5 minutes, but the two remaining flasks were not disturbed.

To determine the uptake of fission products from seawater, croaker and spot were kept in separate tanks containing 50 liters each of radioactive seawater and subsequently analyzed for radioactivity. The fission product concentration was adjusted to 1,000 beta disintegrations per second (dps) per gram of water in each tank. The ages of the fission product mixtures were 186 days in the croaker experiment and 68 days in the spot experiment. Seawater first was filtered through cotton to remove large particles which might have provided an excess of surface area for sorption of fission products. The seawater had a salinity of 32 to 35‰, a temperature of 22 to 26 C, a pH of 7.71 to 7.98, and was aerated continuously.

Gastro-intestinal absorption of fission products by croaker and bluefish from single doses and by bluefish from repeated doses were measured in separate experiments. In the single-dose experiments, 0.5-μc (beta) doses of a 450-day-old mixture were deposited in the stomachs of croaker with a micropipette, and gelatin capsules containing a 216-day-old mixture were inserted into the stomachs of bluefish. In the repeated-dose experiment, 0.017 μc (beta) and 0.007 μc (gamma) doses of a 1-year-old mixture were pipetted into gelatin capsules which contained cracker crumbs to absorb the liquid and prevent softening of the gelatin. Each capsule then was inserted into an incision in a dead shimp tail. The "spiked" shrimp, freshly prepared for each feeding, were randomly distributed in the tank on alternate days for a total of 28 feedings (Table 1). After the first fish sample at 10 days indicated that very little radioactivity had been accumulated, the quantity of fission products in each dose was increased fivefold (beta=0.085 μc, and gamma =0.035 μc).

Each sample consisted of three fish, which were killed by puncturing the brain, homogenized with an equal weight of distilled water. Aliquots of the homogenates were then processed as described below for radioactivity measurements. Samples of various tissues were removed from some of the fish for radioactivity measurements, before the remaining carcass was homogenized. The fission products present in the fish after removal of the digestive tract were considered to have been assimilated. Tissues and 1- to 2-g portions of homogenized carcass were digested in warm nitric acid in 50-ml beakers, transferred to 10-ml volumetric flasks, and made up to volume with distilled water. Aliquots of 5 ml each were evaporated to dryness in plastic dishes and measured for gross beta activity. Aliquots of 2 ml each were pipetted into glass vials and measured for gross gamma activity.

Gross beta activity was measured with a Geiger-Müller tube having an efficiency of 7.7% as calibrated with a Tl^{204} standard. Gross gamma activity was measured with a well-type scintillation detector having an efficiency of 31.0% based on a Cs^{137} standard. Both standards were obtained from the National Bureau of Standards. Identical conditions of geometry were maintained for all samples counted in either system. Measurements of the fission product stock indicated a slow rate of decay, so no correction was made during the relatively short time the experiments were conducted. Results are expressed either as disintegrations per second or as percentages of the dose.

TABLE 1.—*Summary of repeated doses of a fission product mixture in shrimp meat fed to bluefish on alternate days*

Elapsed days	Cumulative dose (microcuries) per fish	
	Beta	Gamma
9	0.45	0.20
21	2.83	1.62
31	4.74	2.81
43	6.99	4.20
55	10.32	6.29

PARTICULATE NATURE OF FISSION PRODUCTS IN SEAWATER

The uptake of fission products by aquatic organisms depends, in part, upon the availability of the fission products. In the aquatic environment these products may be available to fish from the water and from the organisms which comprise their food. Since availability is governed by the physical-chemical form of the fission products, particle formation in seawater by one of the mixtures was examined prior to conducting the uptake experiments.

Rapid settling of radioactive particles in both Millipore- and cotton-filtered seawater was indicated by the decrease of beta and gamma radioactivity at the surface of the standing seawater (Figure 1). The decrease in radioactivity in the agitated water was attributable entirely to sorption of fission products on the surfaces of the container, since the activity in suspension or solution was distributed homogeneously when sampled. Settling of radioactive particles occurred much more rapidly in the cotton-filtered seawater than in the Millipore-filtered water. Apparently both beta and gamma activity became associated with particles already present, and the larger particles settled more rapidly. As may be surmised from the decrease of radioactivity near the surface of the Millipore-

Table 2.—*Assimilation and loss of beta and gamma radioactivity from the digestive tract of croaker with time, expressed as percentage of a single dose of fission products*

Fate of radio-activity	Elapsed time (hours)							
	4		24		48		96	
	Beta	Gamma	Beta	Gamma	Beta	Gamma	Beta	Gamma
Assimilated	14.1	12.5	7.3	5.6	3.6	3.2	5.0	5.6
Digestive tract and contents	72.0	79.0	9.5	5.9	6.1	0.9	0.8	1.3
Lost	13.9	8.5	83.2	88.5	90.3	95.9	94.2	93.1

filtered seawater, the fission products, in addition to becoming sorbed onto the glass surfaces, either formed particles or became associated with new particles being formed.

In both types of filtered water, larger percentages of gamma emitters than beta emitters were removed from the surface layers by sorption and settling (Figure 1). In Millipore-filtered water settling and sorption reduced the initial gamma activity at the surface 52% and beta 41%. In cotton-filtered water the initial gamma activity was reduced 76% and beta 64%. Both flasks of cotton-filtered water that had not been agitated previously were agitated mechanically for 30 minutes and resampled on the 22nd day. A comparison of the surface radioactivity in the water which had been standing for 22 days and then agitated, and that of the water agitated periodically, indicated that the vigorous agitation did not increase the radioactivity in the standing water to the same level as that in the regularly agitated water. This indicated that more radioactivity was firmly fixed to the surfaces of the container of standing water.

UPTAKE FROM SEAWATER

Uptake of 68-day-old fission products by spot and uptake of 186-day-old fission products by croaker are shown in Figure 2. Neither species reached a very high concentration. Activity of the seawater was rapidly reduced in both experiments, but more rapidly in the croaker experiment, involving the older fission product mixture. Undoubtedly much of the activity loss was due to sorption of some radionuclides in the mixture to the surfaces of the tank. This sorption process occurred even though the seawater was agitated constantly by aeration and by the swimming movements of the fish.

UPTAKE FROM A SINGLE ORAL DOSE

A relatively small proportion of orally administered fission products was taken up by gastro-intestinal absorption in croaker. The maximum amount was assimilated 4 hours after administration (Table 2). Elimination occurred rapidly, 83 to 88% of the dose being lost within 24 hours. The low proportion of assimilation and the rapid loss rate indicate that a large portion of the fission products probably was particulate. After 96 hours, 93 to 94% of the dose had been lost.

Greatest concentration of the assimilated fission products was in the internal organs (Table 3). The remainder of the fish (muscle, bone, skin, scales, eyes, nervous system, and

Table 3.—*Uptake of beta and gamma radioactivity with time by tissues of the croaker following a single dose of fission products (expressed as dps/g)*

Tissue	Elapsed time (hours)							
	4		24		48		96	
	Beta	Gamma	Beta	Gamma	Beta	Gamma	Beta	Gamma
Skin	23	10	88	36	18	12	5	3
Muscle	15	13	86	44	15	11	33	26
Internal organs[1]	180	151	231	105	171	62	160	82
Bone	60	14	144	52	74	16	65	11
Carcass	123	58	50	21	23	14	28	21

[1] Excluding the digestive tract.

TABLE 4.—*Assimilation and loss of beta emitters from the digestive tract of bluefish with time, expressed as percentage of a single dose of fission products*

Fate of radio-activity	Elapsed time (hours)				
	½	1	2	4	8
Assimilated	0	6	2	3	1
Digestive tract and contents	100	90	76	15	3
Lost	0	4	22	82	96

fins) concentrated very little of the radioactive material. The ratio of beta to gamma activity in the different tissues varied considerably without a definite pattern. For example, the beta-gamma ratio in muscle tissue was approximately 1 : 1 after 4 hours and 2 : 1 at 24 hours. After 96 hours, the beta-gamma ratio of bone was approximately 6 : 1, probably due to selective uptake of strontium 90. Because of the complexity of the fission product mixture, however, it would be impractical to attribute much significance to the changes in the beta-gamma ratio in the various tissues. Metabolic usefulness, turnover, translocation, physical decay, and the physical state of the individual radionuclides could have contributed to these changing ratios (beta-gamma ratio of the dose was 1.8 to 1.0). Uptake of beta and gamma radioactivity by bluefish was similar to that of croaker. Bluefish assimilated a maximum of 6% of the dose in 1 hour and excreted 96% after 8 hours (Table 4).

UPTAKE FROM REPEATED ORAL DOSES

Since the previous experiments demonstrated that only a small portion of the fission products was concentrated by fish from single doses, this experiment was designed to test whether or not repeated doses would affect the levels of concentration in bluefish tissues. Measurements of uptake in each sample were compared with the cumulative dosage at the time the sample was taken.

The maximum percentage of assimilation of the cumulative doses occurred on or before 10 days, when 7% of the beta and 8.3% of the gamma emitters were assimilated (Table 5). Less than 1% of the cumulative dose was in the digestive tract at each sampling time. At the end of 55 days, 95.9% of the cumulative gamma dosage and 96.8% of the cumulative beta dosage had been lost. These results, on a percentage basis, are not greatly different from those in the single-dose experiments.

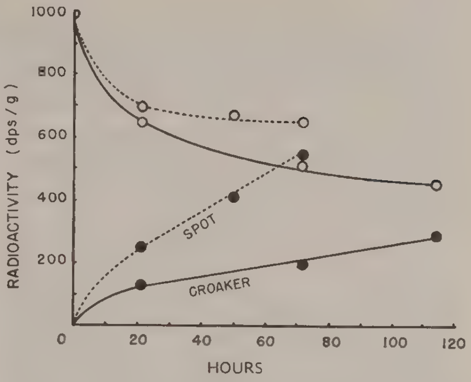

FIGURE 2.—Uptake of fission products by spot and croaker from seawater. (● uptake by fish, o loss from water in the corresponding experiments.) Data for croaker from Rice, Baptist, and Price (1964).

Uptake of radioactivity by the various tissues occurred at a slow rate during the first 10 days but increased considerably thereafter as a result of the increased doses (Figure 3). Of the tissues tested, kidney and liver attained the highest concentrations of both beta and gamma emitters. Differences among the concentrations in the other tissues were only slight. Although approximately 1.5 times more beta than gamma radioactivity was available (Table 1), beta concentration in most tissues was only slightly higher than gamma, except on the 55th day. Since rate of decay of beta and gamma emitters was approximately equal in the fission product stock, it may be assumed that there was some preferential uptake of gamma emitters.

DISCUSSION

Fish accumulate relatively small amounts of fission products, as indicated by the present experiments and the published reports of radiological surveys in the natural environment (Welander, 1955; Donaldson, 1960; Berner et al., 1962). Among the reasons for this are that most fission products are not essential to metabolism and that many, being

TABLE 5.—*Assimilation and loss of beta and gamma radioactivity from the digestive tract of bluefish with time, expressed as percentage of a cumulative dose of fission products*[1]

Fate of radio-activity	Elapsed time (days)							
	10		31		43		55	
	Beta	Gamma	Beta	Gamma	Beta	Gamma	Beta	Gamma
Assimilated	7.0	8.3	3.7	4.5	2.8	3.8	3.0	3.4
Digestive tract and contents	0.3	0.6	0.6	0.8	0.3	0.6	0.2	0.7
Lost	92.7	91.1	95.7	94.7	96.9	95.6	96.8	95.9

[1] See Table 1.

particulate in seawater, cannot pass through living membranes. Another reason is that naturally occurring elements with metabolic properties similar to some fission products are abundant in seawater (for example, K vs. Cs^{137}) and therefore are taken up more readily. Particulate elements probably are adsorbed to a slight extent on fish but to a great extent on phytoplankton. Different species of phytoplankton concentrated Ce^{144} from 2,000 to 4,500 times that in seawater, and the particulate form was taken up at a faster rate than the ionic (Rice and Willis, 1959).

The high concentration of fission products by phytoplankton probably accounts indirectly for the presence of radioactivity in fish in many reported instances. Since fish accumulate only small amounts of fission products directly from seawater, where the radioactivity is quickly diluted and dispersed in the environment, it is likely that accumulation is predominantly from the food chain. Results from operation "Wigwam" demonstrated no significant concentrations of radioactive materials in fishes except in the stomach and gut regions (Berner et al., 1955), indicating that uptake was from ingested water or food, or both. Some radioisotopes that occur in the particulate form in seawater have been found in the internal organs of fish, birds, and other animals (Palumbo, 1961). Palumbo therefore postulated that these radioelements must have been converted to the soluble form at some point in the food cycle. This appears feasible, since the solubility of most fission products is affected by the pH. I have demonstrated, for example, that 6.3% of the Ce^{144}—Pr^{144} in a solution at pH 8.5 passed through a dialysis membrane, 29.5% in a solution at pH 7, and 57.5% in a solution at pH 2. I also have measured the pH of stomachs of 10 croaker 20 hours after feeding and found the mean value to be pH 3.35, which is within

TABLE 6.—*Relative radioactivity contributed by fission products of biological interest at different times after slow-neutron fission of* U^{235}

Isotope	Physical half-life	Percentage of total radioactivity[1]				Percentage ionic in seawater[2]	Percentage absorbed on ingestion[3]
		70 days	200 days	250 days	438 days		
Sr^{89}	54 days	10.1	7.8	6.1	1.4	87	30
Sr^{90}—Y^{90}	28 years, 64 hours	<1.0	<1.0	<1.0	2.5	87	30
Y^{91}	58 days	11.9	10.2	8.5	2.0	0	–
Zr^{95}	65 days	13.6	14.1	12.2	4.9	1	0.01
Nb^{95}	35 days	14.0	25.0	23.0	10.2	0	0.01
Ru^{103}—Rh^{103}	41 days, 57 hours	7.5	3.7	2.3	<1.0	0	20
Ru^{106}—Rh^{106}	1 year, 2 hours	<1.0	1.1	1.5	2.8	0	20
Cs^{137}—Ba^{137}	30 years, 2.6 min	<1.0	<1.0	<1.0	2.0	70	100
Ba^{140}	13 days	3.7	–	–	–	–	5
La^{140}	40 hours	4.0	–	–	–	–	–
Ce^{141}	32 days	10.0	1.9	<1.0	–	2	0.01
Pr^{143}	14 days	4.7	–	–	–	–	–
Ce^{144}—Pr^{144}	282 days, 17 min	4.7	13.1	16.9	30.0	2	0.01
Pm^{147}	2.6 years	<1.0	2.2	3.1	7.4	–	0.01

[1] Adapted from data of Hunter and Ballou (1951).
[2] Greendale and Ballou (1954).
[3] Langham (1960).

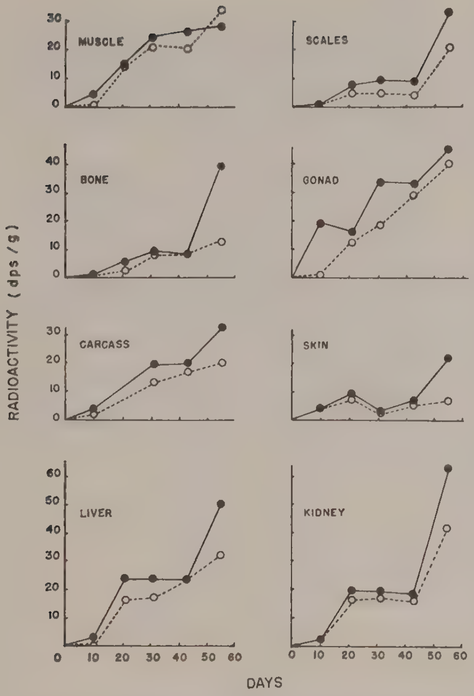

FIGURE 3.—Uptake of radioactivity by bluefish tissues from doses of a fission product mixture given in food on alternate days. (● beta emitters; ○ gamma emitters.)

the range reported for other fishes (Brown, 1957).

Although radionuclides accumulated by the fish in these experiments were not identified, their presence can be surmised by considering characteristics of the individual radionuclides and factors affecting their accumulation. Radioisotopes which represent a small proportion of the mixture, have a short physical half-life, occur as particles in seawater, or are not absorbed after ingestion are not likely to be accumulated to any great extent. By ruling out the isotopes in Table 6 that have combinations of the above factors, it is possible to select the isotopes most likely to have been accumulated. For the 450- and 365-day-old mixtures these would include Sr^{90}—Y^{90}, Ru^{106}—Rh^{106}, Cs^{137}—Ba^{137}, Ce^{144}—Pr^{144}, and Pm^{147}. These isotopes would apply also for the 186-, 216-, and 248-day-old mixtures along with Zr^{95}, Nb^{95}, and Ru^{106}—Rh^{106}. For the 68-day-old mixture all the isotopes in Table 6 would be included except possibly Ba^{140}, La^{140}, and Pr^{143}.

The published literature appears to bear out these assumptions. Rice, Baptist, and Price (1964) demonstrated the presence of Ce^{144}—Pr^{144} in internal organs and Sr^{90}—Y^{90} in bone of croaker by measuring the transmission of beta particles through aluminum absorbers. Aside from neutron-induced isotopes, the only significant concentrations of fission products in minnows in the Columbia River were Cs^{137} in muscle and $Sr^{89,90}$ in bone (Davis et al., 1958). Flounder collected near the Windscale Plant in England contained Sr^{90} and Ru^{106}—Rh^{106} (Dunster, 1958). In the Pacific bomb-testing areas, fish contained relatively small amounts of $Sr^{89,90}$, Cs^{137}, Ru^{106}—Rh^{106}, Zr^{95}, Ce^{141}, and Ce^{144}—Pr^{144}, but the largest proportion of radioactivity was attributable to Zn^{65}, a neutron-induced radionuclide (Rinehart et al., 1955; Thomas, Reid, and Lust, 1958). Clams accumulated fission products to levels ranging from a concentration factor of 1 for $Ru^{103,106}$ and Sr^{89} to 13 for Zr^{95} and 280 for rare earth elements (Gong et al., 1957).

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Electrophoretic Analysis of Hemoglobins of California Rockfish (Genus *Sebastodes*)

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Multiple hemoglobins from 27 species of rockfish (*Sebastodes*), collected at San Diego and Monterey, California, were analyzed by starch-gel electrophoresis. Typical electrophoretic patterns for each species are figured. Hemoglobins within two species pairs (*S. caurinus–S. vexillaris* and *S. eos–S. chlorostictus*) are quite different from one another, thus lending support to their distinction as species. In addition, hemoglobin patterns of other closely related species elucidate certain subgeneric groupings within *Sebastodes*.

Introduction

VARIATION in hemoglobins has been demonstrated for a wide variety of animals. In each species for which individual variation has been shown and studied, this hemoglobin polymorphism has been found to be under genetic control. Progeny data on hemoglobin systems have not been available for species of fish. However, data for fish populations have readily lent themselves to genetic interpretation and have conformed to Hardy–Weinberg principles (Sick, 1961). It is therefore a reasonable assumption that hemoglobins in fishes are, as in other species of animals, controlled by genes.

Hemoglobins, as proteins, have certain specific mobilities in an electric field. This mobility is governed by the charge and size of the molecule, and by the electrophoretic conditions to which the molecule is subjected. As such, electrophoretic mobility is a convenient and important characteristic for hemoglobins. Electrophoretic patterns of hemoglobins are thus useful for purposes of racial and taxonomic studies, and are an important tool in the study of biochemical systematics (Tsuyuki, Roberts, and Vanstone, 1965).

Tsuyuki, *et al.* (1965) analyzed electrophoretically hemoglobins and muscle myogens of eight species of *Sebastodes* from British Columbia waters. In this study, we report on the electrophoretic analyses of the blood of 27 species of California rockfish, and discuss the significance of the results with respect to the identification and taxonomic separation of some of the species.

The rockfishes (*Sebastodes*) constitute the largest genus of fishes in the eastern north Pacific with over 50 recognized species. Most were described prior to 1900, although a species new to science was reported as recently as 1964 (Fitch). Proper identification of the rockfishes has long been a problem. Phillips (1957) clarified many of the existing taxonomic problems and provided an invaluable guide to rockfish identification. He pointed out the existence of several taxonomically vexatious pairs of species within the genus and suggested that future investigations might result in the synonymy of some of these pairs. We directed particular attention to two of these pairs (*S. chlorostictus–S. eos* and *S. caurinus–S. vexillaris*) with the hope that information on their hemoglobins might help to elucidate taxonomic relationships,

Another perplexing problem of rockfish

taxonomy is the determination of the proper generic status of the group. Phillips (1957) reviewed the numerous attempts which have been made to construct generic groupings for the eastern Pacific rockfishes beginning with Gill (1862), who proposed 2 genera, and ending with Jordan, Evermann, and Clark (1930) who recognized 14 genera. Such attempts have been based largely on incomplete analyses of the total species complement, and current workers refer all the species to the single genus *Sebastodes*, although the presence of certain subgeneric groups is obvious. A purpose of our study was to determine whether the species within these morphologically related subgeneric groups have similar hemoglobin characteristics.

One of the most critical investigations on the generic status of rockfishes was that of Cramer (1895), who studied the cranial characters of 32 different species. He used a number of closely correlated osteological characters to arrange the species within the genus; these included the convexity or concavity of the interorbital area, the strength or weakness of the cranial ridges and spines, and the degree of curvature of the base of the skull. Phillips (1957) used the first two of these as major characters for the separation of species. Our electrophoretic

Table 1. Data for California Rockfish (*Sebastodes*) from which Blood Was Sampled for Electrophoretic Analysis.

Interorbital Area	Species	Date (1965)	Locality	Method	Number Sampled
Convex	*paucispinis*	3/24; 4/19; 5/6	San Diego	pole and line	7
	goodei	4/19	"	"	1
		5/26	"	set line	1
	ovalis	5/6	"	pole and line	5
	rufus	4/19	"	"	1
	hopkinsi	5/6	"	"	1
		6/10	Monterey	"	2
	mystinus	3/24	San Diego	"	1
		6/10; 6/11	Monterey	"	17
	melanops	6/10	"	"	4
	flavidus	6/10	"	"	5
	serranoides	3/24; 5/3; 5/6	San Diego	"	11
	pinniger	6/11	Monterey	"	1
	miniatus	3/24; 5/3	San Diego	"	3
	macdonaldi	4/19	"	"	1
		5/13	"	set line	3
Flat or nearly flat	*levis*	4/19; 5/6	San Diego	pole and line	3
		5/13	"	set line	2
	auriculatus	6/10	Monterey	pole and line	1
	saxicola	5/13	San Diego	set line	2
	rubrivinctus	5/6	"	pole and line	1
		5/26	"	set line	1
	caurinus	6/10; 6/11	Monterey	pole and line	6
	vexillaris	5/3	San Diego	"	2
	elongatus	5/13	"	set line	5
	dallii	5/3	"	pole and line	3
Concave	*rhodochloris*	5/26	San Diego	set line	3
	rosaceus	5/6	"	pole and line	5
	chlorostictus	5/6	"	"	5
	eos	5/13; 5/26	"	set line	18
	constellatus	5/6	"	pole and line	6
	nebulosus	6/11	Monterey	"	1
	serriceps	5/3	San Diego	"	2

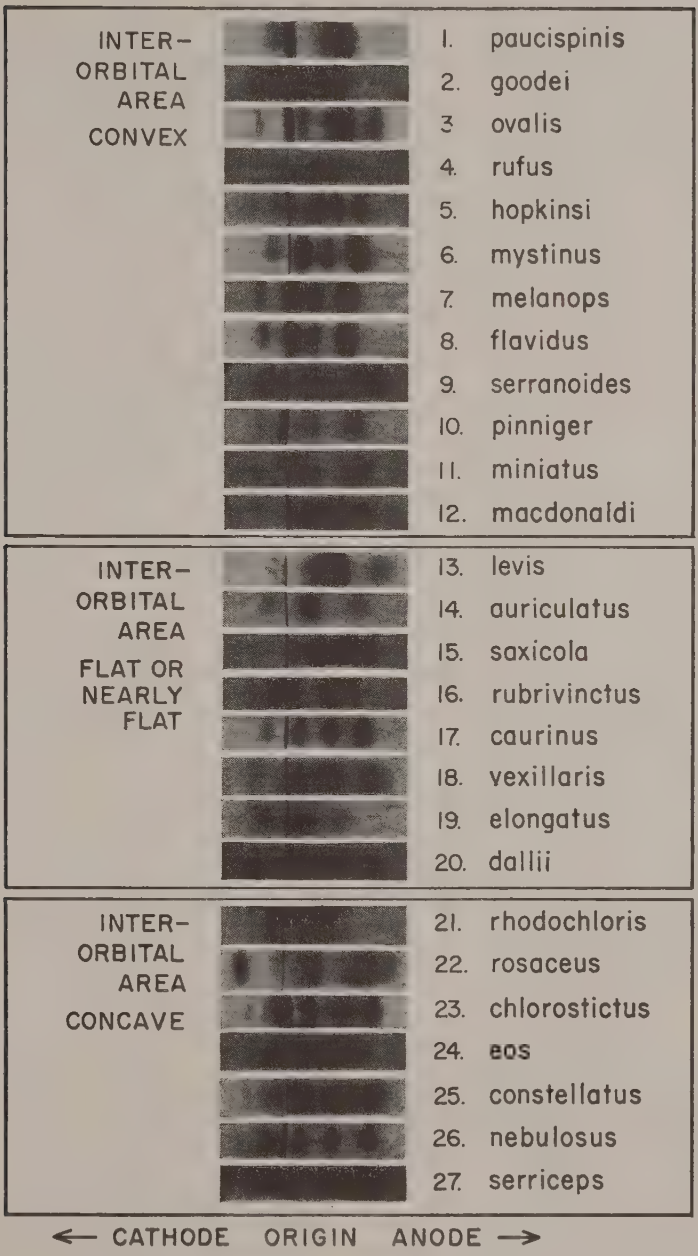

Fig. 1. Electrophoretic patterns of rockfish (*Sebastodes*) hemoglobins.

patterns (Fig. 1) are grouped and listed according to Cramer and Phillips.

METHODS

The 130 specimens of the 27 species of rockfish used for this study were collected off San Diego and Monterey, California from April to July 1965 (Table 1). All specimens were adult except for *S. caurinus*, for which both adults and juveniles were collected, and *S. auriculatus*, which is represented by one juvenile. Phillips' (1957) review of California rockfishes was used to identify species. Blood samples were taken by direct puncture of the caudal artery or vein, with Alsever's solution as the anticoagulant. Except for the samples taken on 24 March and 19 April at San Diego, blood was taken immediately after capture of the fish. On the two days excepted, the fish were held alive for several hours in the bait tank of the vessel, and the blood taken on shore. All the blood samples were held on ice until their analysis 6–12 hr later.

In the laboratory, the blood samples were centrifuged and the clear plasma discarded. The blood cells were washed three times with 1.3% saline, and lysed with equal volumes of distilled water; stroma were removed by centrifugation. The hemoglobins were separated by the starch-gel electrophoretic technique of Smithies (1955), modified by use of different buffer systems. The starch-gel was prepared in a borate buffer solution at pH 8.5; the bridge solution was Tris buffer of pH 9.0. Voltage was maintained constant at 280 v for 3.5 hr of horizontal electrophoresis at 7° C in a field 176 mm long. The gels were stained with Amido black.

Up to 15 samples were run at one time on the same gel. All species could not be run at the same time on the same gel but, as far as possible, the technique was kept constant from gel to gel so that differences in pattern for the same species on different gels were inconsequential.

RESULTS AND DISCUSSION

Typical electrophoretic patterns of the hemoglobins for each of the 27 species are shown in Fig. 1. Where more than one blood sample was analyzed electrophoretically for a species, the pattern with the clearest definition of zones was selected for the figure. Except for possibly *S. eos*, clear genetic polymorphism was not indicated for any of the species examined. However, in many cases only a few individuals of a species were tested and other possible protein patterns may not have been encountered. The variation in *S. eos* is being investigated and will be reported on at a later date. The electrophoretic pattern for the most frequently collected variant of *S. eos* was used in Fig. 1. Only two species, *S. hopkinsi* and *S. mystinus*, were collected both in central and southern California; no difference associated with location was found in the hemoglobin patterns for either species. Although differences between hemoglobin patterns of juvenile and adult fish have been reported (Koch, Bergstrom, and Evans 1964; Vanstone, Roberts, and Tsuyuki, 1964), no differences between patterns for juvenile and adult *S. caurinus* were found in our study.

The number of zones on either side of the origin is tabulated in Table 2 for each species. There is some subjectivity in the enumeration of the zones because of both faintness and incomplete separation of the zones. The counts given in Table 2 were made directly from the original gels; some are higher than those countable from Fig. 1 because of difficulty in photographing the fainter zones.

The total number of recognizable hemoglobin zones in each species, as evidenced by our technique, varies from 2 in *S. rufus* to 10 in *S. chlorostictus* and *S. constellatus*. The hemoglobin zones are distributed on both sides of the origin; cathodal zones range in number from 0 to 4, anodal, from 1 to 6. The numbers of anodal and cathodal zones are positively related, the anodal usually being in the majority. There is no apparent relationship between the total number of zones and the morphological categories that have been recognized within the genus. However, those species with a concave interorbital area have a greater number of zones than do most of the other species.

The hemoglobins exhibit a wide range of mobilities on both sides of the origin. No basic similarity of mobility is evident within any of the three suggested morphological groups, and the morphological trends within the genus proposed by Cramer (1895) are not paralleled by any trend in hemoglobin type.

Table 2. Number of Zones by Species in Electrophoretic Patterns of Rockfish Hemoglobins.

Cathodal Zones	Anodal Zones					
	1	2	3	4	5	6
0		*rufus*	*macdonaldi*		*saxicola*	
1		*levis*	*auriculatus* *elongatus*			
2		*paucispinis*	*nebulosus* *caurinus* *flavidus* *mystinus*	*ovalis* *pinniger*	*dallii* *vexillaris*	*miniatus* *serranoides*
3	*serriceps*		*rubrivinctus* *melanops*	*rhodochloris* *goodei*	*hopkinsi* *rosaceus*	*eos*
4						*chlorostictus* *constellatus*

Species with convex interorbital area.—Similar patterns were found for species within certain small groups listed under each of the three major units. Thus, in those species with a convex interorbital area, a general similarity among the hemoglobins for *S. flavidus*, *S. melanops*, and *S. mystinus* is apparent. The latter two are morphologically similar but their hemoglobin patterns are readily separable on the basis of the greater mobility of *S. mystinus* hemoglobin on the anodal side of the origin. The hemoglobin patterns for *S. melanops* and *S. flavidus* are strikingly similar, except for an extremely faint cathodal zone on the extreme left in *S. melanops* (more apparent in the original gel than in the figure). These two species also are considered by taxonomists to be closely related and, along with *S. serranoides*, have been included by Hubbs and Schultz (1933) in the subgenus *Sebastosomus*. However, the pattern for *S. serranoides* is different from those for *S. flavidus* and *S. melanops*, even though the three species are included in a single subgenus.

Also included in this group are *S. miniatus* and *S. pinniger*, two closely related but valid species. The general similarity of the electrophoretic patterns suggests a close relationship between these two, but *S. miniatus* has one slower-moving and one faster-moving hemoglobin than does *S. pinniger*, confirming that they are two species. Also, in this group, the species *S. ovalis* and *S. rufus* are now considered identical, although current morphological studies (R. Rosenblatt, pers. comm.) show that they are, in fact, separate species. The differences in the protein patterns for the two species confirm the morphological distinction.

Species with flat interorbital area.—In this grouping, *S. caurinus* and *S. vexillaris* are morphologically very similar and are considered as possible synonyms by some workers. While a general similarity in the grouping of anodal zones is evident, *S. vexillaris* has the greater number of hemoglobins, including one (possibly two) more mobile than any of *S. caurinus*. This genetic separation which suggests that these are valid species should be considered in future taxonomic work. Hubbs and Schultz (1933) grouped these two species with six others, including *S. dallii* and *S. nebulosus*, in the subgenus *Pteropodus*. The hemoglobins of *S. dallii* are very similar to those of *S. vexillaris*, as are those of *S. nebulosus* and *S. caurinus*. The general resemblance of all these corroborates the arrangement of Hubbs and Schultz (1933).

Species with concave interorbital area.—*Sebastodes chlorostictus* and *S. eos* are difficult to distinguish from one another by morphological characters. The hemoglobin patterns shown here for the two species are quite dissimilar (as is also the pattern for the variant *S. eos* noted above, but not shown in the figure), which confirms the validity of their distinction as separate species. The patterns for *S. rosaceus*, *S. eos*, and *S. constellatus* are generally similar, especially on the anodal side of the origin; these species, in fact, are members of a clearly recognizable morphological complex which also includes *S. rhodochloris, S. chlorostictus, S. helvomaculatus*, and *S. umbrosus.* The electrophoretic pattern for *S. rhodochloris* is markedly different from others in the group.

With this technique of electrophoretic separation based on the biochemical properties of the multiple hemoglobins of the various species of rockfish it has been possible to indicate groupings of several species in accord with the accepted systematic status of these species, although in some cases the groupings suggested by the similarity of the electrophoretic patterns are inconsistent with those established on morphological grounds; and it has been possible to show genetic separation between some closely related species. The value of these biochemical techniques is strongly indicated.

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TRIGGERFISHES (BALISTIDAE) OF THE EASTERN PACIFIC

By

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ABSTRACT: Six species of Balistidae occur in the eastern Pacific: *Balistes polylepis*, *Pseudobalistes naufragium*, *Sufflamen verres*, *Melichthys niger*, *Xanthichthys mento*, and *Canthidermis maculatus*. These are described and illustrated. The known ranges and general habitats are given for each. Keys are presented to facilitate identification of juveniles and adults. Relationships of these species with balistids from other areas are discussed.

The triggerfishes, family Balistidae, order Plectognathi, are cosmopolitan in warm seas throughout the world and are significant components of the marine environment. They are frequently very abundant in certain areas — occurring epipelagically as developing young, usually benthically or epibenthically as older juveniles and adults. Some of the species are voracious carnivores, others are largely omnivorous. The pelagic young are important as forage fish for predatory species, but the tough-skinned adults are not.

Human use of triggerfish is not great. No significant, selective, commercial fishery exists for them in North America; but they are fished for in some tropical areas, and are frequently caught incidental to other fishing operations. They are often taken in bottom trawls in shallow water and out to depths of 30 or 40 fathoms. They will strike at trolled or cast artificial lures, and take cut bait on hook and line. In some reef or rocky areas where they are abundant,

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they bite or strike bait so readily that they are considered a nuisance by fishermen who seek other species. Most triggerfish probably are scrappy fighters when hooked and give fast and hard action to a fisherman using light tackle. The species of *Balistes* that we have eaten have a very good flavor (*B. capriscus* and *B. polylepis*). The flesh of some species from tropical localities has been reported as toxic.

One major interest in the triggerfishes is the locking and trigger mechanism of the first two spines of the dorsal fin. This has been demonstrated by working models in museums and documented many times in technical and popular publications (see Clothier, 1939).

Several species of triggerfishes are held in high esteem by marine aquarists throughout the world because of their striking color patterns.

The major purpose of this paper is to afford convenient means to identify the juvenile and adult stages of eastern Pacific triggerfishes. Certain warranted changes in scientific names are documented. Protracted prejuvenile stages are described for *Melichthys niger* and *Sufflamen verres*. Sexual dimorphism in pigmentation is described for *Xanthichthys mento* and *Sufflamen verres*. For each species a synopsis is given on general external morphology, ontogenetic changes, distribution in the eastern Pacific, and relationship to extralimital species. Juveniles and adults of each species are illustrated.

Six species of Balistidae occur in the eastern Pacific. *Melichthys niger* and *Canthidermis maculatus* have world-wide distribution. *Xanthichthys mento* is distributed across the Pacific, and has close relatives in the western Indian Ocean and the western Atlantic. *Pseudobalistes naufragium* and *Sufflamen verres* are endemic to the eastern Pacific, but have near relatives in Hawaii and other Indo-Pacific waters. *Balistes polylepis*, currently thought to be an eastern Pacific endemic, is related to a western Atlantic species, but may have closer affinities with an Hawaiian form.

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Methods

Methods of measuring and counting follow those used for Monacanthidae by Berry and Vogele (1961, p. 62, fig. 1) with the following additions:

Standard length (SL): All body lengths are given in millimeters of standard length.

Maximum depth: The greatest vertical measurement, usually through the end of the pelvic process; in specimens with the pelvic fan preserved in an expanded condition, the fan depressed before measuring.

Scale row counts: The number of rows, aligned obliquely dorsoventrally, from upper end of gill opening to end of caudal base; the counts not precise, due to a number of irregular oblique rows and intercalated rows on most specimens.

Pectoral fin rays: The spine at the dorsal origin of the fin not included in the count; this spine prominent in very small specimens, inconspicuous in large specimens; counts recorded from both fins of each fish, but without respect to right or left orientation. [In specimens with one more pectoral ray in one fin than the other, this bilateral variation appears to be random, neither right nor left.]

Gillraker counts: The total number on the lateral side of the first arch on the right side of the fish; arch exposed by an anterior incision from the lower margin of the gill slit; rakers close to the posterior end of the arch often difficult to count.

Vertebrae counts (abdominal + caudal, including the urostyle): The anteriormost caudal centrum defined as that centrum with the posterior margin of its hemal spine touching or in close apposition to the anterior margin of the dorsal portion of the first and enlarged interhemal spine (pterygiophore) of the anal fin. [The dorsal end of the first interhemal spine terminates below the junction of the eighth and ninth centra in two eastern Pacific species, *Melichthys radula* and *Canthidermis maculatus*, and nearly below the center of the eighth centrum in the other four species.]

Incasing scales of the pelvis: A term preferable to the previously used "pelvic spine" to denote the scales incasing the posterior end of the pelvis (see Tyler, 1962, p. 245).

Prejuvenile stage: The pelagic life-history stage of various marine fishes, characterized by morphological structure and appearance noticeably unlike that of the juvenile stage, and by rapid metamorphosis into the juvenile which is much more like the adult (see Hubbs, 1958, p. 282).

Abnormalities that were obvious in some specimens were not included in the general descriptions or tables. In the second dorsal and anal fins of some small specimens it was apparent, from the wide space between the bases of two consecutive rays, that a ray had not formed or had degenerated between these two. In some specimens with a low pectoral ray count on one side, as 15/12 or 13/10, abnormally multiple branching near the bases of several rays on the fin with the low count, suggested that two or more rays may have coalesced during an early stage of development.

Specimens of *Melichthys niger*, *Xanthichthys mento*, and *Canthidermis maculatus* from other than eastern Pacific localities were not used in the frequency distributions of tables 1 and 2.

The following collection abbreviation symbols are used here and in the text: AHF, Allan Hancock Foundation, University of Southern California; ANSP, Academy of Natural Sciences of Philadelphia; BC, Institute of Fisheries Research, University of British Columbia; BLLJ and BLSD, U. S. Bureau of Commercial Fisheries, Biological Laboratories at La Jolla and San Diego; BMNH, British Museum (Natural History); BPBM, Bernice P. Bishop Museum, Honolulu; CAS, California Academy of Sciences; LACM, Los Angeles County Museum; MCZ, Museum of Comparative Zoology, Harvard University; MNHN, Muséum National d'Histoire Naturelle; SIO, Scripps Institution of Oceanography; SU, Natural History Museum, Stanford University; TABL, U. S. Bureau of Commerical Fisheries, Tropical Atlantic Biological Laboratory, Miami; UCLA, University of California at Los Angeles; USNM, United States National Museum.

Generic Synonymy

We have classified the six species of eastern Pacific Balistidae into six genera. We can anticipate disagreement by some of our colleagues with these allocations, and we expect some taxonomists might label our decisions as "excessive splitting" into monotypic genera. Not one of these six genera is monotypic — each contains additional species in other areas of the world.

In the most creditable analysis yet published of generic relationships within the family Balistidae, Fraser-Brunner (1935, pp. 661–663) divided the family into 13 genera. This generic classification has variously been accepted, rejected, or ignored by subsequent authors; some have alternated in their application of Fraser-Brunner's opinions. Recently, de Beaufort (1962, pp. 278–281), dealing with species representing 11 genera by Fraser-Brunner's classifi-

Table 1. *Frequency distributions of numbers of dorsal softrays, anal softrays, and pectoral rays (counted on both sides) for the six species of eastern Pacific Balistidae.*

	Dorsal softrays											
Species	23	24	25	26	27	28	29	30	31	32	33	34
Balistes polylepis				3	18	19						
Pseudobalistes naufragium			3	27	5							
Sufflamen verres								5	19	14	2	
Melichthys niger									1	16	6	3
Xanthichthys mento						1	7	10	5	1		
Canthidermis maculatus	4	20	4									

	Anal softrays										
Species	20	21	22	23	24	25	26	27	28	29	30
Balistes polylepis					4	20	16				
Pseudobalistes naufragium				11	22	2					
Sufflamen verres								2	16	17	5
Melichthys niger								1	2	17	6
Xanthichthys mento						1	7	11	4	1	
Canthidermis maculatus	3	17	7	1							

	Pectoral softrays								
Species	12–12	12–13	13–13	13–14	14–14	14–15	15–15	15–16	16–16
Balistes polylepis			2	2	33	1			
Pseudobalistes naufragium			1	2	30	2			
Sufflamen verres					35	7	1		
Melichthys niger						1	17	1	1
Xanthichthys mento	2	4	18						
Canthidermis maculatus			6	–	20	1			

cation, lumped all of them into the single genus *Balistes*—although he did recognize the 11 generic names in his key to the family and species, seemingly as subgenera.

We accept six of the genera proposed by Fraser-Brunner; we have not studied five others (*Abalistes*, *Balistoides*, *Odonus*, *Balistapus*, and *Rhinecanthus*); and we have reason to reject the other two (*Nematobalistes* and *Verrunculus*), which we consider to be junior synonyms of *Balistes*.

Nematobalistes Fraser-Brunner (monotypic, *B. forcipatus* Gmelin) was distinguished from *Balistes* by "First few rays of first [*sic*, = second] dorsal fin separate, filamentous. Anal fin not elevated anteriorly" (Fraser-Brunner, 1935, p. 659). The relatively great elongation of the first several rays of the second dorsal fin is an ontogenetic process in the late juvenile and adult stages, possibly

Table 2. *Proportions (range in percentage of standard length) of body and fin parts in different length classes of six species of eastern Pacific Balistidae. [Ranges are rounded to the nearest one percent, except for eye diameter.]*

Size (mm. SL)	*Balistes polylepis*	*Pseudobalistes naufragium*	*Sufflamen verres*	*Melichthys niger*	*Xanthichthys mento*	*Canthidermis maculatus*
Head length						
<50	39–40	35	35–38	39	41–47	37–39
50–99	36–39	43	35–38	34	34–39	35–36
100–199	34–36	37–39	37–38	30–32	32	33–34
200–299	34–36	37–40	35–37	29–30	29–30	32–33
300–399	33–34	38	33–35	29	–	–
>399	35	–	–	–	–	30–31
Snout length						
<50	21–23	22	21–23	27	23–26	17–20
50–99	22–24	25	23–25	22	21–24	19–20
100–199	24–25	26–28	28–29	20–21	20	19–21
200–299	25–26	28–30	28–29	20	18–20	18–19
300–399	25	29–30	27–29	19	–	–
>399	26	–	–	–	–	18–19
Eye diameter						
<50	11.8–12.7	8.0	9.6–11.8	9.4	13.2–14.7	12.1–12.3
50–99	9.3–10.5	12.5	8.9–10.8	6.8	8.0–11.0	8.3–9.7
100–199	7.2–8.6	7.7–9.7	6.5–8.3	6.3–7.5	7.2	7.3–8.6
200–299	6.4–7.8	6.9–8.1	5.3–6.4	5.0–5.7	5.5–5.6	6.0–6.9
300–399	5.3–5.4	5.6–6.6	4.1–4.7	3.9	–	–
>399	5.4	–	–	–	–	5.5–5.9
Depth, dorsal to anal						
<50	51–52	55	41–43	36	35–39	45–50
50–99	49–52	60	39–44	39	34	45–48
100–199	49–53	54–57	41–44	42–47	34	41–43
200–299	49–53	52–55	41–46	42–45	33–35	37–39
300–399	49–51	49–51	37–43	43	–	–
>399	53	–	–	–	–	36–37
Depth, maximum						
0–49	59–62	62	54–58	54	49–56	57
50–99	58–60	65	48–50	–	43–45	56
100–199	53–59	56–60	49–50	47–52	–	47
200–299	55–57	57–60	45–52	51	36–42	–
300–399	55–57	56–57	46–50	50	–	–
400+	58	–	–	–	–	37

associated with sexual dimorphism; and we do not believe this or the only moderately lobed anal fin are characters significant enough to warrant generic distinction.

Table 2. Continued.

Size (mm. SL)	*Balistes polylepis*	*Pseudobalistes naufragium*	*Sufflamen verres*	*Melichthys niger*	*Xanthichthys mento*	*Canthidermis maculatus*
Longest dorsal softray length						
<50	15–17	17	11	13	15–17	16–19
50–99	20–23	18	11–12	–	14–15	19–22
100–199	19–29	20–23	14–15	20–24	15	26–28
200–299	25–31	24–26	13–15	17–19	16–19	24–26
300–399	27–28	23–26	14–15	17	–	–
>399	27	–	–	–	–	23–27
Longest anal softray length						
<50	14–17	16	12–13	12	14–17	15
50–99	17–21	16	11–11	–	12–14	19
100–199	16–23	16–19	13	12–16	–	27
200–299	20–25	20–23	12	15–16	16–17	–
300–399	22	22–23	12–13	15	–	–
>399	26	–	–	–	–	22–24
First dorsal spine length						
<50	26–33	26	24–30	30	28–30	18–24
50–99	21–26	31	20–22	20	24–30	18–19
100–199	20–23	22–23	18–20	17–21	22	–
200–299	14–21	19–22	18–20	15–17	10–16	12–14
300–399	17	26	17–18	15	–	–
>399	15	–	–	–	–	10–12
Pectoral fin length						
<50	14–15	17	13–14	13	16–20	14
50–99	13–14	17	12–13	10	12–15	11–13
100–199	12–15	13–14	11–12	10–13	11	11–12
200–299	12–15	13–14	10–11	9–11	11–12	11–12
300–399	11	13–14	8–11	9	–	–
>399	13	–	–	–	–	11

Verrunculus Jordan (monotypic, *B. polylepis*) was distinguished from *Balistes* and *Nematobalistes* by "Scales on body much smaller than those on cheek" (Fraser-Brunner, 1935, p. 659). *Balistes polylepis* has a larger number of body scale rows than does *B. capriscus* Gmelin, and consequently on similar sized specimens the body scales on *B. polylepis* would be the smaller. Squamation on the cheek of *B. polylepis* is highly variable. On a few specimens the cheek scales are relatively large and somewhat symmetrically arranged, so that there appear to be several, narrow, longitudinal, and vertical grooves between the rows of scales; but on most specimens the cheek scales are relatively small and are arranged irregularly, similar to those in *B. capriscus*; and in some specimens the sizes and arrangement are intermediate.

KEY TO ADULT EASTERN PACIFIC BALISTIDAE

A. Five to eight conspicuous longitudinal grooves on cheek below eye .... B
AA. Grooves on cheek absent or inconspicuous C
B. Body scales separated; dark pigment between scales. Figure 13 .... *Xanthichthys mento*
BB. Body scales close together; no dark pigment between scales. Figure 8 .... *Sufflamen verres*
C. Small scales posterior to gill opening, of similar size to other body scales. Figure 16 .... *Canthidermis maculatus*
CC. Enlarged scales posterior to gill opening, much larger than adjoining body scales ...... D
D. Scaleless area on snout behind jaws. Figures 3B and 5 .... *Pseudobalistes naufragium*
DD. Snout completely scaled .... E
E. No longitudinal ridges on posterior part of body. Figure 4 .... *Balistes polylepis*
EE. Eight to ten longitudinal ridges on posterior part of body. Figure 11 .. *Melichthys niger*

KEY TO YOUNG EASTERN PACIFIC BALISTIDAE
(smaller than 100 mm. SL)

1. Dorsal rays 23 or 24 .... *Canthidermis maculatus*
2. Dorsal rays 25
   a. Body depth (dorsal to anal) 45–50 percent SL, 2.0–2.2 into SL .... *C. maculatus*
   b. Body depth (dorsal to anal) 55–60 percent SL, 1.7–1.8 into SL .... *Pseudobalistes naufragium*
3. Dorsal rays 26–27
   a. Snout completely scaled. Dorsal rays modally 27 (table 1) .... *Balistes polylepis*
   b. Snout scaleless posterior to lips (at least as small as 34 mm. SL, possibly not scaleless in smaller specimens). Dorsal rays modally 26 (table 1) .... *P. naufragium*
4. Dorsal rays 28–29
   a. Body depth (dorsal to anal) 49–52 percent SL, 1.8–2.1 into SL .... *B. polylepis*
   b. Body depth (dorsal to anal) 34–39 percent SL, 2.6–2.9 into SL .. *Xanthichthys mento*
5. Dorsal rays 30–34
   a. Pectoral rays 12/12 to 13/13 .... *X. mento*
   b. Pectoral rays 14/14 to 16/16
      i. Pectoral rays modally 15. Snout profile blunter (see fig. 9) ...... *Melichthys niger*
      ii. Pectoral rays modally 14. Snout profile less blunt (see figs. 6 and 7) .... *Sufflamen verres*

Balistes polylepis Steindachner.

Finescale Triggerfish.
(Figures 1A, 2A, 3A, 4.)

Balistes polylepis STEINDACHNER, 1876, p. 69 (type locality, Magdalena Bay, Baja California, Mexico).

Body moderately deep; caudal peduncle laterally compressed; head profile usually slightly convex, occasionally flat or with only a slight convexity over snout.

Scales covering entire body and head (fig. 3A); scales generally of similar size; some slightly smaller scales on head. Most specimens with scales in irreg-

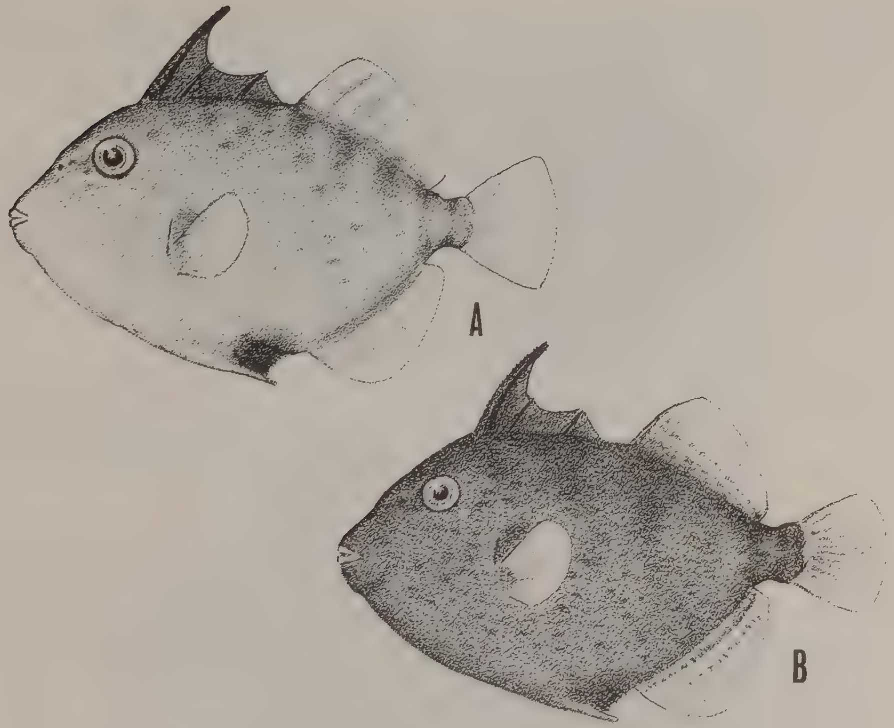

Figure 1. A, *Balistes polylepis*, 38.4 mm. SL, Magdalena Bay, Baja California, Mexico, SIO 60-294. B, *Pseudobalistes naufragium*, 34.4 mm. SL, Banderas Bay, Jalisco, Mexico, BLLJ station B6108-31.

ular arrangement below eye; a few specimens with these scales aligned to form 4 or 5 short, narrow, horizontal and inconspicuous grooves between the scale rows. No ridges on posterior part of body. Enlarged scales (4 or 5) posterior to gill opening. Incasing scales of pelvis forming a movable process. Preorbital groove pronounced.

Teeth with moderately strong cusps, the cusps becoming progressively smoother with growth (cusps worn off median pair of lower jaw teeth at sizes larger than about 150 mm. SL).

D. III, 26–28; A. 24–26; P_1 13–15 (table 1). Third dorsal fin spine not markedly shortened. Soft dorsal fin with a pronounced anterior lobe developing at about 50 to 70 mm. SL. Anal fin with anterior rays longer, but not forming as pronounced a lobe as in soft dorsal fin. Caudal fin rounded to about 70–80 mm. SL, becoming emarginate at larger sizes, and falcate at about 120–150 mm. through progressive elongation of the most dorsal and the most ventral

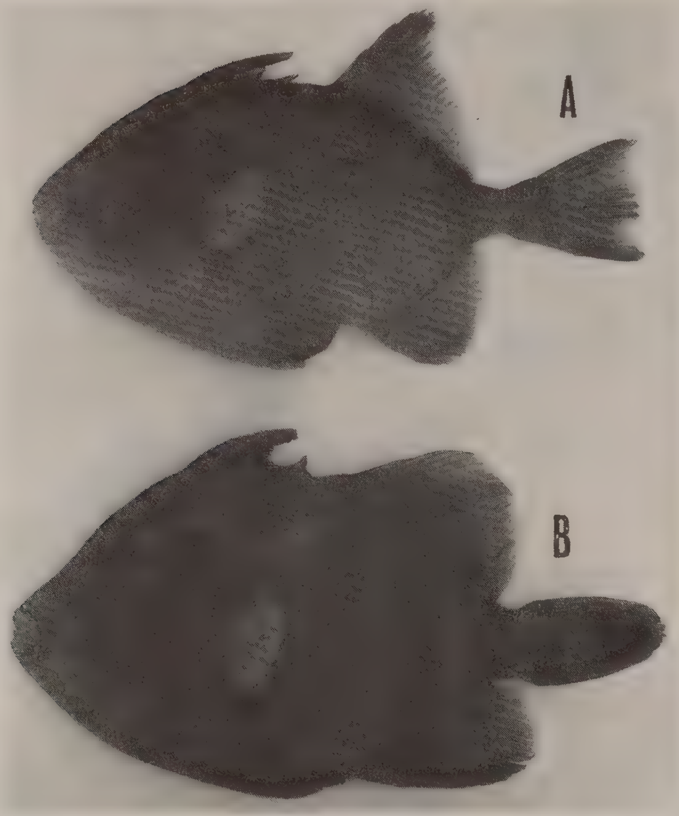

FIGURE 2. A, *Balistes polylepis*, 96.5 mm. SL, Bahia de los Angeles, Baja California, Mexico, SIO 62-236. B, *Pseudobalistes naufragium*, 100.5 mm. SL, Bocochibampo Bay, Sonora, Mexico, UCLA W51-3.

caudal rays. Scale rows 58–62 (8 specimens). Gillrakers 29–37 (12). Vertebrae 7 + 11 (4).

PIGMENTATION. Late juveniles and adults (figs. 2A and 4) generally dark, but lighter on ventral half of head and body; fins dusky with pectorals the clearest; fringed area behind pelvic process darker than other ventral parts of body on some specimens. Juvenile pigmentation persistent to about 100 mm. SL or smaller as large spots below third dorsal spine, soft dorsal origin, and soft dorsal termination. Small pelagic juveniles (fig. 1A) slightly darker on upper part of body, with a characteristic black or very dark dorsal spine membrane and a black area behind the incasing scales of the pelvis; usually four dark areas or spots along the dorsal fin base and three along the anal base, and

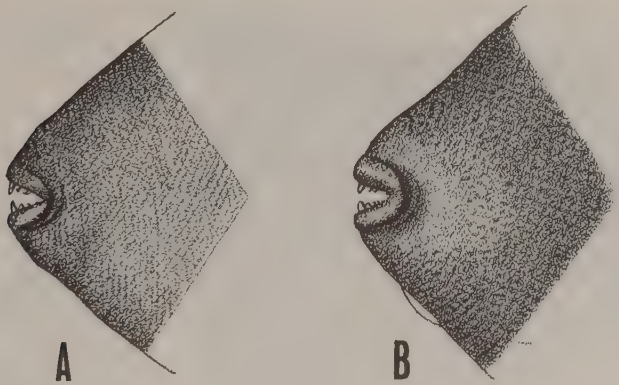

Figure 3. Squamation of snout. A, *Balistes polylepis*, 117 mm. SL, UCLA W54-366. B, *Pseudobalistes naufragium*, 115 mm. SL, UCLA W51-3.

irregular spots scattered over the body; the softrayed fins usually clear, but scattered pigment occurring in fins of some individuals.

Range. This endemic eastern Pacific species has been reported from Lobos de Afuera, Peru (Hildebrand, 1946, p. 481) to San Francisco, California (Radovich, 1961, p. 30). We have examined specimens from Colombia to northern California and from the offshore islands of Malpelo, Galápagos (Charles), Revillagigedo (Socorro), and Tres Marias (Cleopha) — (fig. 17). This species occurs in offshore waters and at oceanic islands but not so frequently as *S. verres*, and it does not have the more oceanic orientation of *Melichthys*, *Xanthichthys*, and *Canthidermis*. The furthest offshore collection, about 110 miles southwest of Panama, consisted of four young, 47.5–108 mm. SL, taken under floating bamboo in a tide rip.

A single specimen, 254 mm. SL, from NW. of Crescent City, California, represents the northernmost record of the species and the family in the eastern Pacific. The specimen (SIO 60-511), taken off St. George Light, 41°50′N., 124°22′W., in water 280 fathoms deep, 20 October 1960, by the trawler "City of Eureka," was given to the Scripps Institution of Oceanography fish collection by the Marine Resources Division of the California Department of Fish and Game on 10 January 1961 (R. H. Rosenblatt, personal communication). We do not know the depth at which the trawl caught this specimen. This record is not shown in fig. 17.

Relationships. Three specimens, 251, 262, and 360 mm. SL, labeled *Balistes fuscus* from Honolulu, Hawaii (ANSP 93826, and BPBM 5013), and the illustration based on another Hawaiian specimen labeled *B. fuscus* by Fowler (1928, pl. XLV, fig. C) are referable to *B. polylepis*. They are not

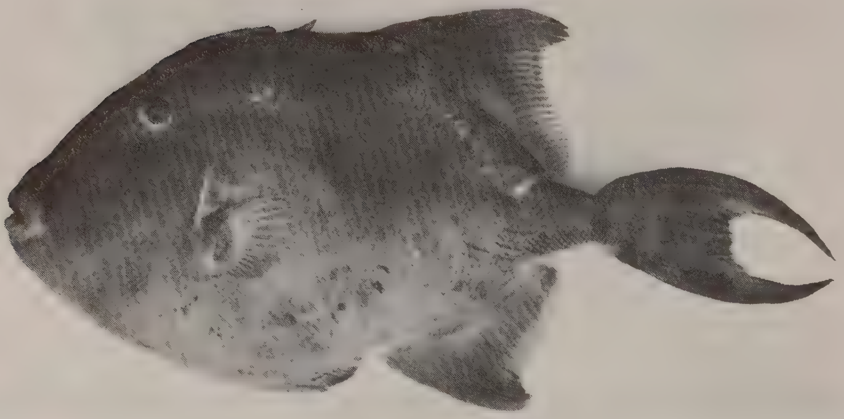

FIGURE 4. *Balistes polylepis*, 442 mm. SL, Marquis Point, Baja California, Mexico, SIO 62-703.

Balistes [= *Pseudobalistes*] *fuscus* Bloch and Schneider 1801, which has a scaleless area on the snout and a relatively shallow preorbital groove. The Hawaiian specimens cannot be identified through the use of two publications on Hawaiian Balistidae (Jordan and Evermann, 1905, pp. 407–418; Clark, 1949, pp. 9, 10), and, although they key out to *B. fuscus* in another (Gosline and Brock, 1960, p. 292), this last treatment is not specific. This species in Hawaiian waters is generally inadequately known or unrecognized. It may also occur in other Indo-Pacific areas, and these uncertainties restrict our analysis of the zoogeography and relationships of the species of *Balistes*.

Balistes polylepis appears to be a "distant" geminate of *B. capriscus* Gmelin of the Atlantic. *Balistes polylepis* tends to have more scale rows and lacks the punctulated stripes on the second dorsal and anal fins of *B. capriscus*. In most specimens of *B. polylepis* the cheek scales are smaller and more irregularly arranged than in *B. capriscus*; but this character varies among individuals in *B. polylepis*, and the cheek scales of a few specimens of *B. polylepis* we have seen are almost identical to those of *B. capriscus*.

Pseudobalistes naufragium (Jordan and Starks).
Smoothcheek Triggerfish, Pez Puerco de Piedra.
(Figures 1B, 2B, 3B, 5.)

Balistes naufragium JORDAN and STARKS in Jordan, Starks, Culver, and Williams, 1895, p. 488 (type locality, Mazatlan, Mexico; holotype 173 mm. SL, SU 1656).

Body moderately deep; caudal peduncle compressed; head profile straight or slightly convex over eye and slightly concave over snout.

Scales normal over most of body; an area around snout becoming scaleless (possibly by absorption or sloughing of scales) — (fig. 3B); extent of scaleless area increasing with growth of fish, about anterior 30 percent of head at 51 mm. SL, about 40 percent at 121 mm., and about 60 percent at 322 mm. Scales on posterior part of head slightly smaller than those on body. Scales in area below eye aligned in indistinct and irregular horizontal or slightly oblique rows (less distinct on larger specimens). No ridges on posterior part of body. Enlarged scales (4) posterior to gill slit. Incasing scales of pelvis forming a movable process. Preorbital groove very shallow and short, scarcely evident.

Teeth with moderately strong cusps; worn off median pair of lower jaw teeth in larger specimens, and these two teeth rounded.

D. III, 25–27; A. 23–25; P_1 13–15 (table 1). Third dorsal fin spine not markedly shortened. Soft dorsal fin with anterior rays forming a slight lobe by about 200 mm. SL, causing the fin to slant downward to the rounded posterior margin. Anal fin rounded with the anterior rays longer, but not forming an anterior lobe, and becoming angulate (sloping backward) in larger specimens. Caudal fin rounded to about 135 mm. SL, becoming biconcave with slightly elongated dorsal and anal lobes at larger sizes. Scale rows about 45–55 (6 specimens). Gillrakers 31–36 (6). Vertebrae 7 + 11 (6).

Pigmentation. Juvenile, 34.4 mm. SL (BLLJ station B6108-31, figure 1B): traces of five body bars, mainly on dorsal part of body; spots scattered over generally dark-pigmented body; dusky row of spots along base and just distal to base of both soft dorsal and anal fins; spinous dorsal fin dark; caudal dusky; pectorals clear. Juvenile, 51 mm. SL (BC 59-674): specimen somewhat faded; six body bars, first two under spinous dorsal and extending only about halfway down side, third under origin of soft dorsal fin, fourth under middle and fifth under termination of fin, sixth on posterior end of caudal peduncle; trace of one narrow band across interorbital area; no scattered spots on body or fins; fins clear except for dusky membranes of the spinous dorsal fin. Juveniles 101–121 mm. SL (6 specimens, UCLA W51-3, fig. 2B): five body bars (the anterior two noted on the 51-mm. specimen apparently fused into one on these and other larger specimens), the first bar interrupted but extending nearly to ventral profile, the other four bars extending to ventral profile; small spots scattered over dorsal half of body; two bands across interorbital area; a short line posterodorsal to eye and a broader line posteroventral to eye extending to first body bar, these lines fused into a solid blotch on some specimens; a small dark fringed area behind pelvic process; spinous dorsal fin dark; pectoral fin nearly clear; the other three fins dusky; scattered spots on posterior parts of soft dorsal and anal fins on one 115-mm. specimen. Other larger specimens examined have these body bars, the fifth bar tending to become obscure. The largest specimen with body bars was 211 mm. (UCLA

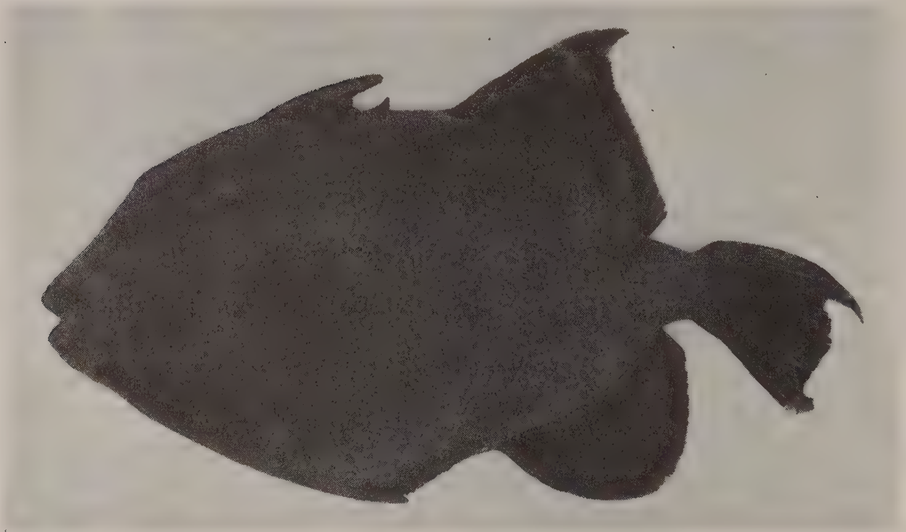

Figure 5. A, *Pseudobalistes naufragium,* 352 mm. SL, Islas Venados, Sinaloa, Mexico, UCLA W51-43.

W56-115), and only the anterior four bars were visible; this specimen was the only one seen that had three bands across the interorbital area (a 203-mm. specimen from the same station had the usual two bands). One collection of three specimens, 118, 164, and 178 mm. SL, from Panama (SU 6877), afforded the suggestion of variation in pigmentation: all have traces of the interorbital bands; the 118- and 164-mm. specimens have five faint body bars; the 178-mm. specimen lacks the bars, and has a mottled pattern of many thin, irregular and wavy, variously directed, dark lines—this last is reminiscent of the lines shown for a specimen of about 135 mm. of *Pseudobalistes fuscus* from the Red Sea by Clark and Gohar (1953, text-fig. 5c). A larger specimen (237 mm., UCLA W56-114) and the two largest specimens examined, 322 mm. (SIO 62-63) and 352 mm. (UCLA W51-43, fig. 5), have no distinctive markings but have generally dark pigment all over with lighter pigment distally on the dorsal and anal softrays.

Range. This endemic eastern Pacific triggerfish is apparently common nowhere. It is known to range from Guayaquil, Ecuador (SU 9305, CAS IU13432a, USNM 53485), to Santa Maria Bay on the western coast of Baja California (UCLA W55-100), and to Bocochibampo Bay, Sonora, on the mainland coast of Mexico (UCLA W51-3). It has not been recorded from the major offshore islands, but has been taken at Isabel Island off Nayarit, Mexico (SIO 62-63). Specimens that Fowler (1944, pp. 298, 412, 526) recorded from "North of Galápagos" and from Isabel Island as *Balistes naufragium* are not this species, but are young of *Balistes polylepis*.

RELATIONSHIPS. Four nominal species were assigned to the genus *Pseudobalistes*, characterized by a scaleless area on the cheeks and a shallow preorbital groove, by Fraser-Brunner (1935, p. 663). De Beaufort (1962, pp. 305–306) recognized two of these species as valid, *P. fuscus* (Bloch and Schneider) and *P. flavimarginatus* (Rüppell), both ranging from eastern Africa eastward to the Tuamotu Islands; *P. fuscus* ranging northeastward to Hawaii. De Beaufort considered the third species, *P. chrysospilos* (Bleeker), to be a junior synonym of *P. fuscus*. The fourth nominal species listed by Fraser-Brunner, *P. naufragium*, one of three valid species of *Pseudobalistes*, is most closely related to *P. fuscus*, which was briefly defined and finely illustrated from Red Sea specimens by Clark and Gohar (1953, p. 28, text-figs. 5a, 5b, and 5c; pl. I, fig. 1). *Pseudobalistes naufragium* and *P. fuscus* have similar numbers of fin rays, but differ appreciably in the pigmentation pattern of their juvenile stages.

Sufflamen verres (Gilbert and Starks)

Carr's Triggerfish, Coche.
(Figures 6, 7, 8.)

Balistes verres GILBERT and STARKS, 1904, p. 153, pl. XXVI, fig. 49 (type locality, Panama; holotype SU 6805).

Body moderately elongate and shallow; caudal peduncle compressed; snout and head profile generally straight, sometimes slightly concave anterior to front of eye and convex above eye.

Scales covering entire head and body. Seven or eight horizontal grooves below eye, irregular and pronounced, but shallow; enlarged scales in single rows between the grooves; scales anterior and posterior to this area slightly smaller than scales on remainder of body. Area on sides from about a vertical at soft dorsal fin origin to caudal base with about 10 to 14 horizontal, interrupted ridges formed by elevated processes on anterior angle of scales. Enlarged scales (3 or 4) behind gill slit. Incasing scales of pelvis movable. Preorbital groove moderately deep and pronounced.

Teeth with moderate to strong cusps, the cusps usually worn almost smooth on medial teeth of large specimens, especially in lower jaw.

D. III, 30–33; A. 27–30; P_1 14–15 (table 1). First dorsal spine thick; third spine short, but not markedly reduced. Soft dorsal and anal fins without pronounced fin lobes, fourth or fifth rays the longest. Caudal fin truncate to about 180 mm. SL, becoming emarginate at larger sizes with the most dorsal and ventral rays slightly produced. Scale rows 52–57 (3 specimens). Gillrakers 27–31 (4). Vertebrae 7 + 11 (3).

ONTOGENY AND PIGMENTATION. *Sufflamen verres* exhibits sexual dimorphism in pigmentation and has a characteristic spotted prejuvenile stage.

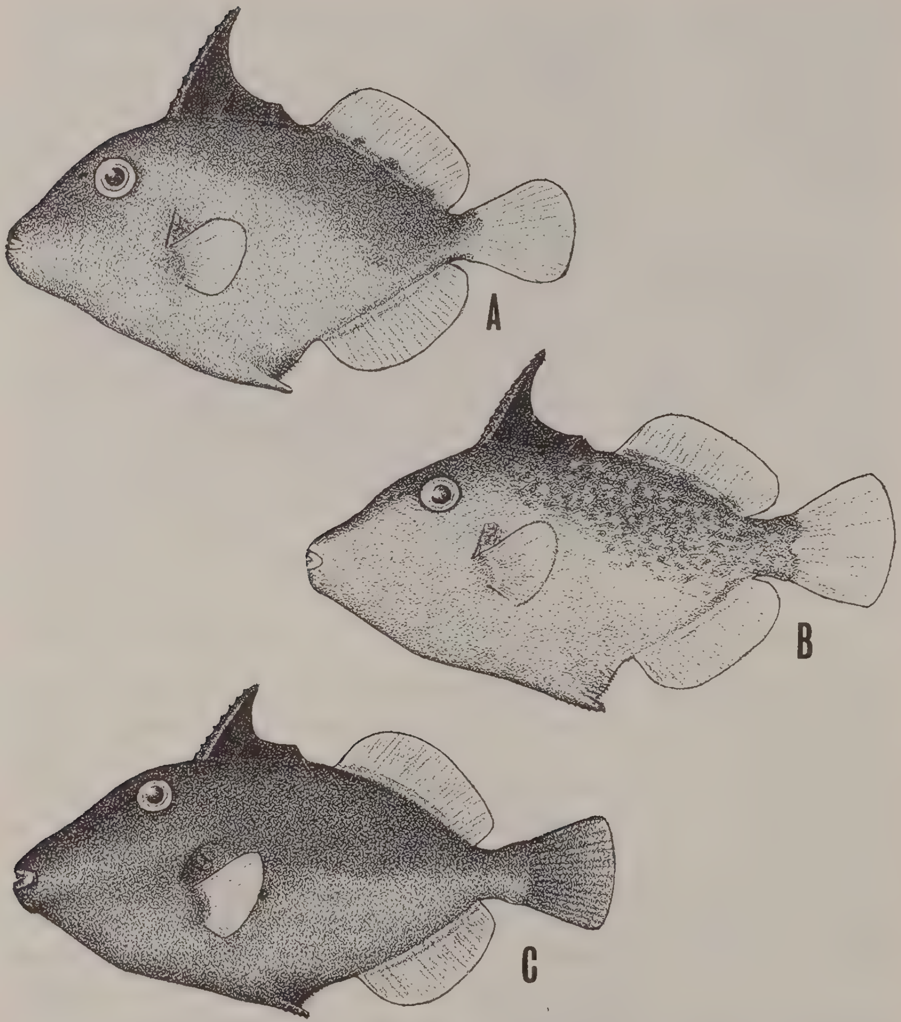

Figure 6. *Sufflamen verres*. A, 26.0 mm. SL, 69 miles off Acajutla, El Salvador, UCLA W58-222. B, 46.5 mm. SL, Clipperton Island, UCLA W56-161. C, 54.6 mm. SL, Ceralbo Island, Gulf of California, Mexico, UCLA W61-34.

In the smallest juveniles examined, 12.6 mm. (UCLA W60-139) to 26 mm. SL, the body is dark on the upper part and light on the lower, with three or four spots developing along the base of the dorsal fin (fig. 6A). Spots begin to develop on the upper part of the body at about 26 mm., and this "late" or spotted prejuvenile stage probably persists to an average length of about 55 mm. (as in fig. 6B). It may extend in a "protracted" prejuvenile stage, to at

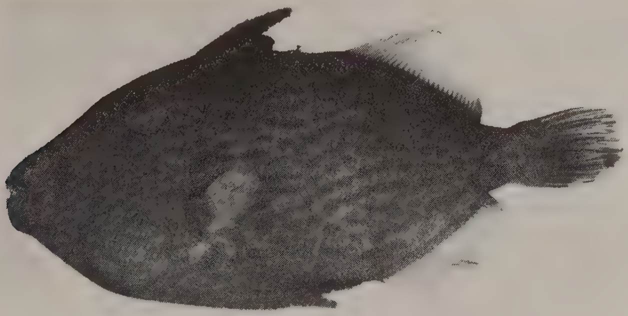

Figure 7. *Sufflamen verres*, 64 mm. SL, Clipperton Island, SIO 62-341.

least 75.5 mm. (BC 60-464, as in fig. 7), or transformation to the unspotted juvenile stage may occur in specimens as small as 50.5 mm. (UCLA W61-34, as in fig. 6C). In the protracted prejuvenile stage, the spots tend to elongate into an irregular series of broken lines (fig. 7); in the largest specimen of this stage, the broken stripes are restricted to an area just above each pectoral fin, and are visible only when the specimen is wet.

In some of the smaller juvenile specimens, the body is almost uniformly dark brown. In others, the lower part of the body is lighter (fig. 6C).

The pigmentation of males and females is similar in pattern but is very different in intensity. In males the dark upper body parts are darker and the lower body parts much lighter than in females (fig. 8). In males the throat is very light and the lower half of the body from the peduncle to near the pelvic fins is only slightly darker. The line on each side from the posterior angle of the lips to below the gill slit, and the band extending under the throat and connecting these two lines, are very pronounced in males, but are generally vague or not apparent in females. The pronounced pigmentation pattern was present in 17 males, 197–375 mm., and the pale pigmentation in 30 females, 141–342 mm. The sex of these 47 specimens was determined by gross examination of the gonads. In an additional 27 specimens, 100–204 mm., we either could not locate gonads or could not determine sex.

The liver was extremely large, almost filling the body cavity, in two specimens of the protracted prejuvenile stage, 62 and 65 mm. (CAS 6036). In juvenile specimens of similar lengths and in many adults examined, the liver was relatively much smaller.

Relationships. *Sufflamen verres* is closely related to *S. fraenatus* (Latreille) [= *S. capistratus* (Shaw) = *S. mitis* (Bennett)] which ranges from Hawaii westward to South Africa. The two species are very closely similar in morphology and in adult pigmentation. Specimens of *S. fraenatus* from the

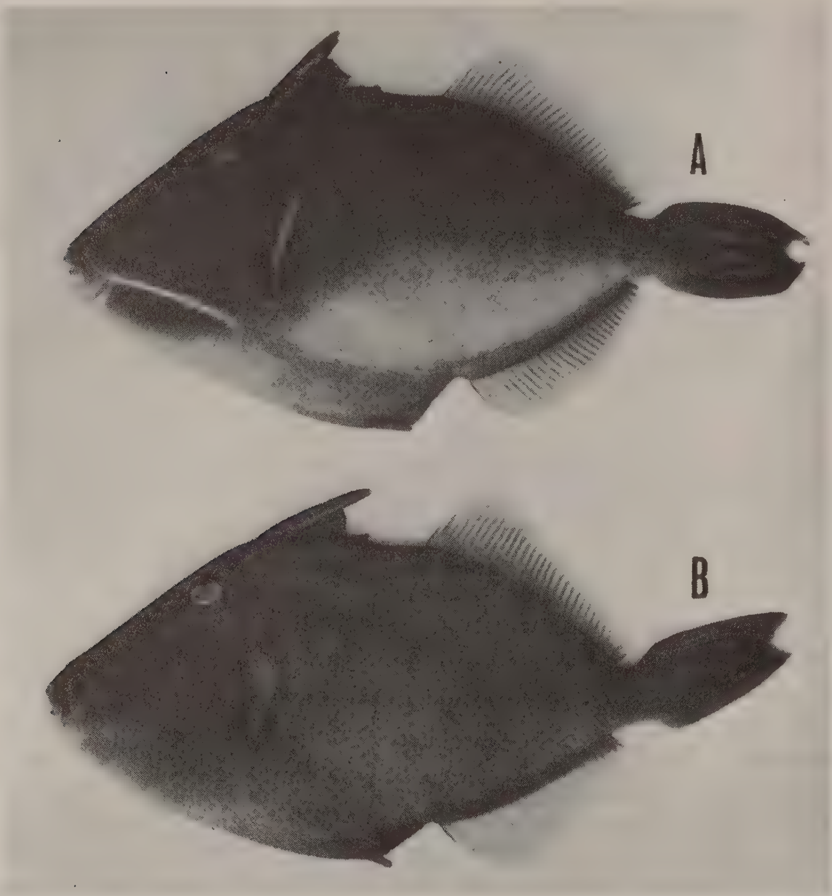

FIGURE 8. *Sufflamen verres*. A, male, 206 mm. SL. B, female, 210 mm. SL. Punta los Custodios, Nayarit, Mexico, UCLA W58-37.

central Pacific have a lower number of softrays (about D. 28–30, A. 24–26) than *S. verres* (table 1); but a specimen of *S. fraenatus* (ANSP 101164) from South Africa, at the western extreme of the range, has D. 31 and A. 27, very similar to *S. verres*.

RANGE. This endemic eastern Pacific species is known to range along the American continent from Salinas, Ecuador (Orces, 1959, p. 89), to near Cedros Island, western Baja California, Mexico (SU 57245). It occurs at most of the offshore islands — the Galápagos, Cocos, Clipperton, Revillagigedos, and Tres Marias Islands — and has been taken well offshore as developing young. The northernmost record for the species, near Cedros Island, is based on a

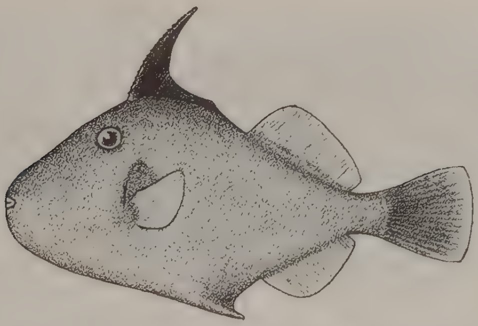

Figure 9. *Melichthys niger*, 47.4 mm. SL, Clarion Island, UCLA W55-163.

30.5-mm. SL prejuvenile, collected November, 1937 by the ZACA, and labeled as "food of *Makaira mitsukutii*."

Melichthys niger (Bloch).

Black Triggerfish, Black Durgon, Galafate.

(Figures 9, 10, 11.)

Balistes nigra Osbeck, 1757, p. 295 (species name pre-Linnean and not available; type locality "Assensionen").

Balistes niger Bloch, 1786, p. 27, pl. CLII, fig. 2; plate incorrectly labeled *Balistes ringens*; type locality, "? chinesischen Gewässer").

Le Baliste Sillonné Lacépède, 1798, p. 370, pl. 18, fig. 1 (vernacular name only; type locality "Mers des Indes"; cited as *Balistes sillone* Lacépède with holotype A. 8497 in Muséum National d'Histoire Naturelle according to Le Danois, 1961, p. 519).

Balistes radula Solander in Richardson, 1848, p. 21, pl. 6, figs. 1–4 (type locality, Pacific Ocean?).

Balistes kibitar Thiollière, 1857, p. 216 (type locality, Woodlark Island; according to Fowler, 1928, p. 455).

Balistes piceus Poey, 1863, p. 180 (type locality "Havane").

Melichthys bispinosus Gilbert, 1890, p. 125 (type localities, Clarion and Socorro Islands).

Balistes fuscelineatus Seale, 1901, p. 9, fig. 4 (type locality, Honolulu; holotype no. 664 and paratype in Bernice P. Bishop Museum according to Fowler, 1928, p. 455).

Body moderately elongate; caudal peduncle compressed; head profile concave above eye, slightly convex above snout on some specimens.

Scales covering entire head and body; no grooves between scale rows below eye; scales on body posterior to soft dorsal fin origin with keels forming 8 to 10 longitudinal ridges. Enlarged scales (4 or 5) behind gill opening. Incasing scales of pelvis movable, tending to become fixed in large specimens. Preorbital groove moderately deep and pronounced.

Teeth with cusps in young specimens becoming truncate with growth, especially on the medial teeth (see below).

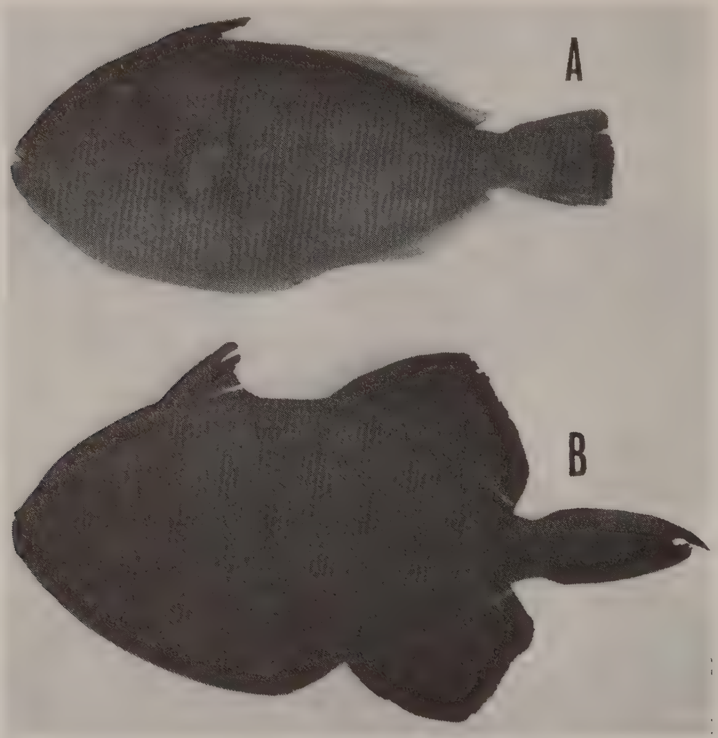

FIGURE 10. *Melichthys niger.* A, prejuvenile, 121 mm. SL, Cocos Island, UCLA W55-52. B, juvenile, 125 mm. SL, Clipperton Island, UCLA W56-236.

D. III, 31–34; A. 27–30; P_1 14–16 (table 1). Third dorsal spine small, very small and recessed below the dorsal profile at sizes larger than about 130 mm. SL. Soft dorsal and anal fins with the anterior rays longest, but without a pronounced lobe. Caudal fin biconcave at about 128 mm. Scale rows 52–54 (3 specimens). Gillrakers 33–39 (3 specimens). Vertebrae 7 + 11 (4 specimens), 7 + 12 (in one apparently normal specimen, UCLA W53-126).

ONTOGENY AND PIGMENTATION. The eastern Pacific specimens examined represent four growth stages that differ in morphology and pigmentation:

Early prejuvenile (1) 47.4 mm. SL (UCLA W55-163).

Late prejuvenile (4) 91, 121, 128, 144 mm. (SIO 62-341; UCLA W55-52, W51-266; BC 57-143).

Transforming prejuvenile (1) 127 mm. (BC 56-329).

Juvenile and Adult (42) 90, 96.5, 97, 99, 107, 108, 108, 113, 118, 119, 124, 126, 126, 159 mm., and 28 larger specimens.

The early prejuvenile specimen (fig. 9) differs in body shape and in having less pronounced pigmentation than the late prejuveniles.

The late prejuvenile specimens (fig. 10A) are dark on the upper part of the body and lighter below and have clear dorsal and anal fins and six or seven narrow dark orbital bands radiating from the eye (the 4 median bands usually join across the top of the head). Single specimens, similar to these, with clear fins, light bodies, eye bands, and cusped teeth have been examined from Hawaii (ANSP 88511), the Tuamotu Islands (CAS uncataloged), and Aves Island west of Dominica in the Caribbean Sea (TABL, OREGON station 4987).

In the characteristic black juvenile and adult stages, the body and fins are entirely black except for areas of the dorsal, anal, and caudal fins (fig. 11). A narrow white stripe (sometimes described as blue) extends along the base of both the dorsal and anal fins. The caudal fin is progressively lighter from the caudal base posteriorly to a dark lunate bar that extends from the dorsal to the ventral lobe; this bar has a narrow, pale posterior margin followed by a broader and slightly darker area at the distal edge of the fin. A series of nine specimens from a collection from Cocos Island (BC 56-329) contains the single transforming prejuvenile (127 mm.) and eight dark juveniles (90–126 mm.). The four smallest of these (90–97 mm.) have visible orbital bands, and the black pigmentation is not so intense as in the larger prejuveniles (107–126 mm.). The orbital bands are apparent in juveniles up to 118 mm., but are very indistinct in slightly larger specimens, and are not visible in most specimens larger than 126 mm. They apparently are only obscured by the black body pigmentation, for in a very old and very faded specimen of 247 mm., eight orbital bands are apparent (USNM 5988).

In the transforming prejuvenile specimen the body is uniformly brownish, the dorsal and anal fins are less brownish, and the narrow, clear basal area in both fins (that will become the white stripe in the juvenile) is apparent; the orbital bands are detectable but vague.

The color in life of a prejuvenile specimen was given by Seale (1901, p. 9, fig. 4), under the name of *Balistes fuscolineatus*. Color of the adults in life was excellently described by Randall (1955, p. 220), under the name of *Melichthys buniva*, and notes on live coloration were given by Jenkins (1903, p. 483).

The genus *Melichthys* has been characterized as having teeth lacking cusps or points. Tooth structure changes are associated with transformation from the prejuvenile to the juvenile stage. The prejuveniles have pronounced cusps on all teeth, but these are generally more rounded in the larger prejuveniles. The smaller juveniles (90–126 mm.) generally show a progression of rounding of the cusps with increase in size; the median pair of teeth in the upper jaw become truncate. Teeth in the lateral parts of the jaws never become entirely truncate, but retain evidence of the prejuvenile cusps. The smallest juvenile observed with truncate teeth was 113 mm. The largest juvenile with pro-

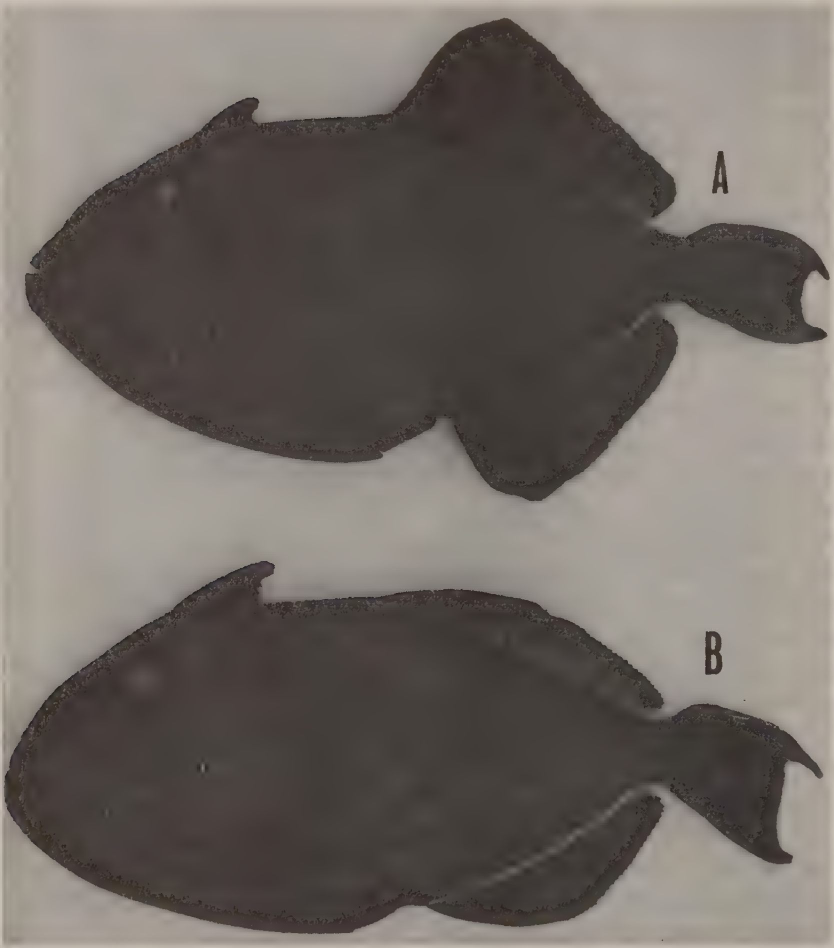

FIGURE 11. *Melichthys niger*. A, female, 206 mm. SL. B, male, 203 mm. SL. Cocos Island, SIO 59-334.

nounced, unrounded tooth cusps was 108 mm. The change in tooth shape probably represents a change in habitat and feeding habits.

The head profile of adults is variable. Most have a slight notch under the lower jaw, as does the female in fig. 11A. The male in fig. 11B has a blunt, rounded snout, but this may not indicate sexual dimorphism, for several other males have the same head shape as the female in fig. 11A. The size ranges of specimens for which we were able to determine sex were: males, 183–306 mm., and females, 192–230 mm.

The liver was relatively much larger in seven late prejuvenile specimens than in several juveniles and adults. A similar situation was observed in *S. verres*. We have not examined this feature in detail, but it suggests some interesting problems of physiology.

Range. A circumtropical oceanic species, usually associated with oceanic islands. In the eastern Pacific known only from Malpelo, Cocos, and Clipperton Islands and from Clarion and Socorro Islands in the Revillagigedo Islands. We have examined specimens from each of these localities (fig. 18). A specimen was reported from between Cocos Island and Panama, at 7°00′N., 84°10′W., by Clemens (1955, p. 166), but we have been unable to locate it to verify the identification. Rosenblatt and Walker (1963, p. 102) indicated that *Melichthys* had been collected on the mainland of western America, but we have not located or confirmed the record. There is a suggestion that this species may have occurred on the mainland. Girard (1858, p. 338) mentioned specimens of balistids collected at San Diego, California, by A. Cassidy that "were of a jet black tint, with light (either white or yellow) margined fins"—these specimens were lost prior to 1858 in moving a large collection of fishes to the Smithsonian Institution. Although we consider it unlikely, it is possible that these lost specimens mentioned by Girard could have been *M. niger*, for oceanic conditions off San Diego in the 1850's were different from those of recent decades (see Hubbs 1949, p. 464).

We have not thoroughly investigated details of the world-wide distribution of *M. niger*. The range was recorded by de Beaufort (1962, p. 284) as, "Sumatra (Priaman); Menado? — Durban, Delagoa Bay, Zanzibar, Seychelles, Mauritius, Ceylon, Christmas Island, China, Philippines, Pacific eastwards as far as Cocos Island, tropical Atlantic." De Beaufort further stated that the only specimen known with certainty from the Indo-Australian Archipelago was that from Priaman, Sumatra, recorded by Bleeker; however, we can confirm as *M. niger* the description of a prejuvenile specimen (under the name of "? *Melichthys buniva*") from Menado, Celebes, by Koumans (1953, p. 262). Fowler (1928, p. 455) reported specimens from a number of central Pacific localities — Thorton Island, Tuamotus, Johnson Island, Marshall Islands, Honolulu, Hawaii, Marcus Island, French Frigates Shoal, Gardner Island, Necker Island, Wake Island, and Lysan Island.

Relationships. We consider that three species comprise the genus *Melichthys*:

Melichthys niger (Bloch) is described above.

Melichthys vidua (= *Balistes vidua* Solander in Richardson, 1844, p. 128, pl. 59, figs. 9, 10; type locality, Otaheiti = Tahiti; probable holotype in BMNH, according to Günther, 1870, p. 217). This species ranges from South Africa eastward to Hawaii and the Tuamotu Islands. Its pigmentation is characterized by a black (or brown) head, body, and first dorsal fin; the caudal fin and posterior part of the peduncle clear, with a thin black margin around the caudal fin on some specimens; and clear second dorsal, anal, and pectoral fins with a narrow black margin around the second dorsal and anal fins and on the distal part of the pectoral fins. Seven to 10 longitudinal ridges occur on the peduncle and posterior part of the body. All teeth have well developed cusps in most specimens examined up to 156 mm. SL, but in the largest specimen examined, 215 mm. (BC 60-220), the median teeth are truncate and the lateral teeth have smooth cusps. We have not observed a prejuvenile stage of this species, but the smallest specimen examined, 92 mm., in a series with five other specimens, 99–156 mm. (USNM 168545-50), has the lightest body pigment of any we have seen. This species has been placed in the genus *Balistes* by most authors, who have at the same time placed *niger* (as *radula*) in *Melichthys*.

Melichthys nycteris (= *Pachynathus nycteris* Jordan and Evermann, 1903, p. 199; type locality, Honolulu; holotype 133 mm. SL, USNM 50821). We have examined three specimens of this species, the holotype, a 95-mm. specimen from Honolulu (ANSP 77704), and a 93.5-mm. specimen from off Thailand in the Andaman Sea (ANSP uncataloged). Fowler (1928, p. 450) recorded two specimens from Honolulu in the B. P. Bishop Museum [Fowler's plate XLIV, fig. B, labeled *Balistes vidua*, is *M. nycteris*]. Fowler (1946, p. 213, fig. 73) described another specimen of this species as a proposed new genus and new species, *Oncobalistes erythropterus*, from Aguni Shima, Riu Kiu Islands (holotype ANSP 72087). The pigmentation of this species is characterized by a black (or brown) head, body, and peduncle; the caudal fin dusky to relatively clear; the pectoral fins clear with a narrow, dusky posterior margin; and the second dorsal and anal fins with narrow dark margins and with three or four narrow longitudinal stripes in the second dorsal fin and with two such stripes in the anal fin. Orbital bands, similar to those in *M. niger*, are visible on the smallest specimen. The three specimens examined have about 14 indistinct, longitudinal ridges on the posterior part of the body and peduncle, and all teeth have well developed cusps.

The following mean fin ray counts suggest intraspecific and interspecific differences in the three species of *Melichthys*:

	Number	Dorsal	Anal	Pectoral
M. niger, eastern Pacific	26	32.4	29.1	15.1
M. niger, central-western Pacific	24	32.5	29.3	15.2
M. niger, Atlantic	6	33.4	30.0	16.1
M. vidua	11	33.4	29.4	14.1
M. nycteris	3	33.3	29.7	14.3

In this small sample, *M. niger* from the Atlantic averages one more ray in each fin than *M. niger* from the Pacific, and *M. vidua* and *M. nycteris* average one fewer pectoral ray and one more dorsal ray than Pacific *M. niger*.

SYNONYMY. *Melichthys niger* (Bloch 1786) is the earliest available name for this species, and we consider it to be the valid name. We discovered this name, originally proposed as *Balistes niger,* and used it for the species in an early 1964 draft of this manuscript. Later that year we concluded that *Balistes niger* Bloch, 1786, had not been used as senior synonym since it was originally described, and we concluded that it presumably qualified as a *nomen oblitum* under the somewhat inexact provisions of Article 23(b) of the International Code of Zoological Nomenclature (1961, p. 23).

In late 1964, W. I. Follett advised us that, under the provisions of the second edition of the International Code of Zoological Nomenclature Adopted by the XV Congress of Zoology (1964, p. 11), the name *Melichthys radula* (Solander in Richardson, 1848, p. 22) was the valid name for this species. This name was not valid according to Article 11(d) of the first edition of that Code (1961, p. 11), because it had originally been described, however incorrectly, in synonymy of another species (see below). The 1964 edition of the Code validated *Balistes radula* Solander, because "prior to 1961" it had "been treated as an available name with its original date and authorship" and it had been "adopted as the name of a taxon."

Three factors have now (15 July 1966) made us reject *Balistes radula* Solander and accept *Balistes niger* Bloch as the valid name for the black triggerfish. Article 23(b) of the Code has been suspended by the International Commission of Zoological Nomenclature (W. I. Follett and Lillian J. Dempster, personal communication). The name *Melichthys niger* (Bloch) has been published as the senior synonym of this species by Mago Leccia (12 July 1965, p. 411). The rejection of *radula* in favor of *niger* does not overtly contravene the desired principle of stability in nomenclature, because, although *radula* has most frequently been used for this species, the species name has also frequently been confused (see below).

Osbeck (1757, p. 295) defined this species and published its first Latinized binomial, *Balistes nigra,* based on specimens from Ascension Island in the South Atlantic Ocean. One year later, in the initial nomenclaturally acceptable publication in zoology, Linnaeus (1758, p. 329) incorrectly included Osbeck's *Balistes nigra* in synonymy of the species that Linnaeus named *Balistes ringens* [recognized by us as *Xanthichthys ringens*]. Linnaeus (1766, p. 409) repeated this error, with the addition to synonymy of the reference to Gronow's manuscript. The "thirteenth edition" of Linnaeus's Systema Naturae, edited and emended by Gmelin (1788, p. 1469), adhered to Linnaeus's prior usage and added several references in synonymy, including the description of *Balistes niger* by Bloch (1786, p. 27 and pl. 152, fig. 2).

In the meantime, Osbeck's 1757 work had become nomenclaturally acceptable through two post-1758 translations. In the translation to German (1765, p. 386) by Georgi, *Balistes nigra* of the original publication was replaced by *Balistes ringens.* In the introduction to his translation of the German edition to English (1771, vol. 1, p. x), Forster stated that Osbeck had revised and made additions to the German translation. Presumably then, Osbeck adhered to Linnaeus's opinion of 1758 and substituted "*ringens*" for "*nigra*" in the 1765 edition. In the English edition (1771, vol. 2, p. 93) this name was given as "*BALISTES ringens* Linn. *Nigra* Osbeck," where the reference to the original use of "*nigra*" by Osbeck was apparently inserted by Forster.

Bloch (1786, p. 27–28, pl. CLII, fig. 2) described and illustrated this species, and his is the earliest nomenclaturally acceptable name we can locate. He cited Lister (in Willughby) as the first to publish on this species and Willughby (1686, app., p. 21; app., pl. I, fig. 24) as the first to illustrate it. Bloch recognized that his *Balistes niger* was identical with a fish described by Osbeck, but he referred only to the post-1758 translation of Osbeck (1765, p. 386, where Osbeck's name was given only as *Balistes ringens*), and he erroneously considered Osbeck's description to have been based on specimens from China. Because Bloch did not refer to the 1757 and 1771 editions of Osbeck (where "*nigra*" was used), we consider that he was proposing a new specific name for this species, and that authorship of "*niger*" should be credited to Bloch. De Beaufort (1962, p. 283) placed "*niger*" of Bloch in questionable synonymy of "*radula*" Solander.

Additional confusion was introduced when the figure complementing Bloch's description of *B. niger* (pl. CLII, fig. 2) was incorrectly captioned "BALISTES RINGENS." The figure is a creditable portrayal of *M. niger*, although it shows five truncate teeth on the right side.

In a publication two years after Bloch's, Bonnaterre (1788) capitalized on this awkward situation. His description of "LE SILLONÉ 10. *B. ringens*" (p. 19) is of *Xanthichthys*, and the habitat was given as "L'Isle de l'Ascension." He copied Bloch's figure of *M. niger* (which Bloch had incorrectly labeled *B. ringens*) to illustrate this (pl. 12, fig. 39, as "Le Sillonné"). Then Bonnaterre proposed *B. niger* as a new name to identify his "LE BALISTE NOIR" (p. 19, pl. 85, fig. 352), which according to the illustration and to de Beaufort (1962, p. 288) is the species currently recognized as *Balistes* [*Balistapus*] *conspicillum* Bloch and Schneider 1801.

In the treatment by Bloch and Schneider (1801, p. 472), *M. niger* was described and discussed in the genus *Balistes* under the specific name of "VINGENS."

Swainson (1839, p. 325) perpetuated the problem by listing the first species under his new genus, *Melichthys*, as "ringens. Bl. pl. 152.2." Bloch's species has been considered as the type species of *Melichthys* by most revisers of Swainson. The proper designation of this type species should be *Balistes ringens* Bloch (not Linnaeus), 1786, pl. 52, fig. 2 = *Balistes niger* Bloch 1786, p. 27. Günther (1870, p. 227) attempted to emend Swainson's genus to a subgenus with the spelling of *Melanichthys*.

Günther (in Playfair and Günther, 1866, p. 135) gave the specific name of

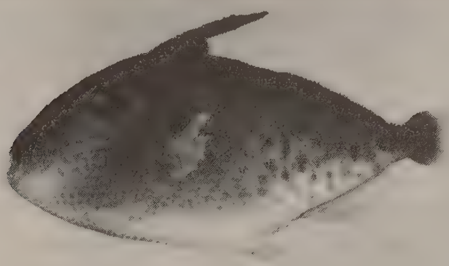

Figure 12. *Xanthichthys mento*, 55 mm. SL, Clipperton Island, UCLA W58-281.

this species as "*niger*," which he considered to be a classical emendation of Forster's addition of "*Nigra*" to the 1771 translation of Osbeck. Günther did not refer to the 1786 work of Bloch, and later (1870, p. 227), he still further confused the issue by incorrectly considering the *Balistes buniva* of Lacépède to be a senior synonym of this species.

In addition to the publication of "*niger*" by Bloch and by Bonnaterre as a new specific name for different species of Balistidae, there are at least two other such proposals: *Balistes niger* Mungo Park (1797, p. 37) is currently recognized as *Balistes* [*Sufflamen*] *chrysopterus* Bloch and Schneider 1801; and *Xenodon* (*Balistes*) *niger* Rüppell (1835, p. 53, pl. XV, fig. 2), currently recognized as *Balistes* [*Odonus*] *erythrodon* Günther 1870 (according to de Beaufort, 1962, pp. 292 and 295).

Richardson (1848, p. 21, pl. 6) described and illustrated this species under the name of *Balistes ringens* Bloch, based on the figure by Bloch (1786, pl. CLII, fig. 2). At the conclusion of his treatment, Richardson published, for the first time and in synonymy of *Balistes ringens*, the name and description of *Balistes radula* Solander from Solander's manuscript, *Animalia Oceani Pacifici*. The 1964 edition of the Code affords validation of *Balistes radula* Solander, because "prior to 1961" it had "been treated as an available name with its original date and authorship" and it had been "adopted as the name of a taxon." The first published use of *Melichthys radula* (Solander 1848) in the above context that we have found is by Jenkins (1903, p. 483). The use of this name was perpetrated by Snyder (1904, p. 534) and by Jordan and Evermann (1905, p. 417), and this is the name that subsequently has been applied most often to the species (see de Beaufort, 1962, p. 283).

Two other names have been used a number of times for this species: 1) *Balistes buniva* Lacépède (1802, pp. 668–670, pl. 21, fig. 1; type locality, Nice, France). The description and illustration are not of a *Melichthys*. Briggs

(1961, p. 554) was correct in suggesting that Lacépède's *buniva* should be retained in synonymy of *Balistes capriscus* Gmelin (1788), but *M. buniva* frequently has been used for *M. niger* in the Pacific (see Clark, 1949, p. 9 and fig. 2, not p. 2; Gosline and Brock, 1960, pp. 294 and 343). 2) *Balistes piceus* Poey (1863, p. 180). This is a junior synonym of *M. niger*, and often has been applied to this species in the West Indies (see Jordan, Evermann, and Clark, 1930, p. 493).

Xanthichthys mento (Jordan and Gilbert).

Redtail Triggerfish.

(Figures 12, 13.)

Balistes mento JORDAN and GILBERT, 1882, p. 228 (type locality, Clarion Islands, Revillagigedos; holotype USNM 28387).

Xanthichthys gotonis TANAKA, 1918. TANAKA, 1935, p. 481, pl. CXXXI, fig. 372 (type locality, Sagami Sea) [male].

Xanthichthys purus TANAKA, 1918. TANAKA, 1935, p. 484, pl. CXXXII, fig. 374 (type locality, Sagami Sea) [female].

Body moderately elongate and shallow; caudal peduncle moderately compressed; snout and head profile convex, almost straight on some specimens.

Scales covering head and body. Conspicuous horizontal grooves on cheek below eye, usually five grooves of which the three median ones are the most pronounced, occasionally six and rarely four grooves; a single row of enlarged scales between each groove. Diagonal grooves between scales on body, less pronounced than those on cheek. Area on sides posterior to soft dorsal fin origin with about 10 to 13 weak, irregular ridges produced by spinules on scales. No enlarged scales behind gill opening. Incasing scales of pelvis movable. Preorbital groove moderately deep and pronounced.

Teeth with strong cusps, the cusps slightly reduced on the two lateral pairs of upper jaw teeth in large specimens, and all teeth with a dark tinge in larger specimens; median pair of upper jaw teeth smaller than adjacent pair.

D. III, 28–32; A. 25–29; P_1 12–13 (table 1). Third spine of dorsal fin minute at all sizes, not extending above the dorsal surface of the body. Soft dorsal and anal fins developing slightly produced anterior lobes by 54.5 mm. SL, the 3rd or 4th rays the longest in the fins. Caudal fin rounded in small specimens, becoming bifurcate by about 100 mm., dorsal and anal lobes produced. Scale rows 42–43 (3 specimens). Gillrakers 40–47 (5). Vertebrae 7 + 11 (3).

PIGMENTATION. Sexual dimorphism exists in pigment pattern of adults.

Males (fig. 13A). The dark head contrasts with the lighter body. The throat and ventral surface of the body are slightly lighter than the rest of the body. A small rounded dark spot occurs in the center of most of the lighter colored scales on the body and throat; the interscale grooves are a contrasting darker shade as are the dorsal and anal fin sheaths. The soft dorsal and anal fins are nearly clear (unpigmented); the proximal parts of a few of the rays are dusky. The pectoral fins may be slightly dusky. The caudal fin is dusky with an almost clear lunate margin.

Females (fig. 13B). The pigmentation is generally darker than in males. There is little contrast in head and body pigment density (as with males). The ventral surfaces are slightly lighter than the remainder of the body. Small rounded spots occur on a few scales of some specimens, but these are usually indistinct. The dark grooves between the scales are more pronounced than in males. The soft dorsal and anal fin rays are pigmented throughout their length, and the interradial membranes are clear, so that the fins appear dark distally. Pigmentation of the pectoral and caudal fins is similar to that in the males, except that the clear distal margin of the caudal is slightly wider in females.

Small juvenile specimens are dark above and light below; the interspinous membrane is black with a smaller clear area around the second spine, the other fins are clear; dark spots form on the upper part of the sides by 23.6 mm. SL; these spots increase in number and extend down the sides in larger juveniles (fig. 12).

Tanaka (1918) described two new species of *Xanthichthys* and later (1931, p. 5) recognized the type specimens as different sexes of the same species (Tanaka placed his *X. gotonis* and *X. purus* in synonymy of *X. lineopunctatus*; we consider them to be junior synonyms of *X. mento*). Tanaka's colored drawings of these two specimens (1931, pl. II) show appreciable differences in coloration, the male with a red tail, yellow body with light blue spots, and a deep blue head, and the female with a yellowish tail, bluish green body, and light blue head.

The description of the "coloration in spirits" of the holotype of *X. mento* indicates that this was a female. The type specimen was searched for in the U. S. National Museum on 9 March 1964 but was not found.

Range. Primarily oceanic, particularly around oceanic islands, and presumably ranging across the entire north Pacific. We have examined specimens taken at a number of offshore localities in the eastern North Pacific from Guadalupe Island to Clipperton Island (fig. 19). *Xanthichthys mento* has been reported from Santa Catalina Island and San Diego, California, by Jordan (1919, p. 2; 1924, p. 82). The occurrence of this species at Easter Island in the eastern South Pacific (USNM 65700, MCZ 29627), and its apparent absence between there and Clipperton Island, suggest an antitropical distribution in the eastern Pacific. If *X. mento* occurs at Cocos or the Galápagos Islands, it should have been collected there. This species was reported to be "Not common" at Hawaii (Gosline and Brock, 1960, p. 293), but United States museums contain a number of Hawaiian specimens, and the smallest specimens of *Xanthichthys* we have seen were caught in Hawaiian waters (18.2–21.5 mm. SL; USNM 118057, SIO 60-253). We have not checked many other records

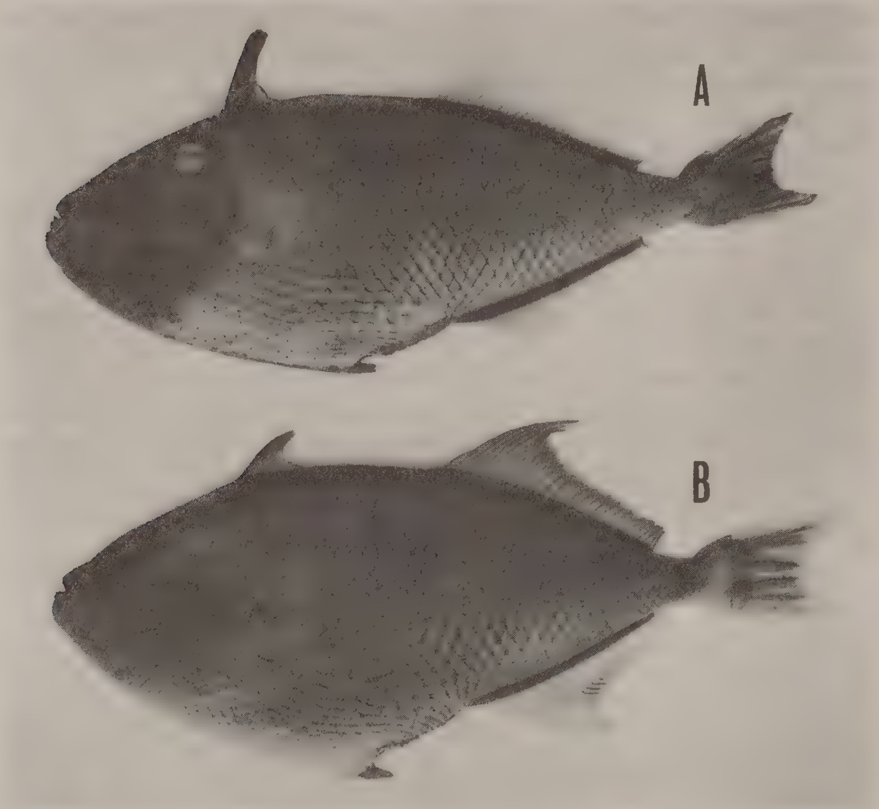

Figure 13. *Xanthichthys mento.* A, male, 203 mm. SL, UCLA W52-82. B, female, 208 mm. SL, UCLA W52-141. Both from San Benedicto Island, Revillagigedo Islands.

of this species from the central and western Pacific. Kuroda (1961, p. 70, fig. 2) described the live coloration of a specimen (as *X. lineopunctatus*) from Zensu Island (30°56′N., 138°49′E.). Kamohara (1957, p. 55) reported on a specimen (as *X. lineopunctatus*) from Ankyaba, Amami-Oshima, Japan. Fowler (1928, p. 451) recorded a specimen (as *B. ringens*) in the U. S. National Museum from Fiji, collected by the Wilkes Expedition, although this was not recorded in his later list of "The fishes obtained by the Wilkes Expedition, 1838–1852" (Fowler, 1940, p. 797). We presume the record from Nauru to represent *X. mento* on the basis of its distribution, although the two specimens recorded from there were only listed (as *Xanthichthys ringens* (Linné)) and were not described (Whitley and Colefax, 1938, p. 299).

Relationships. We tentatively conclude that the genus *Xanthichthys* contains three species.

Xanthichthys ringens (Linnaeus 1758) in the western Atlantic is characterized by two or three pigmented grooves below the eye and dark spots at the apices of most of the body scales. This name is not definitive. Linnaeus' description (1758, p. 329) was based on at least two species, one which we consider to be the western Atlantic *Xanthichthys*, and the *Balistes nigra* of Osbeck (1757) from Ascension Island with the valid name of *Melichthys niger* (Bloch). Linnaeus' earlier account of *Balistes ringens* (1754, p. 58) is also confusing, because it was based in part on Willughby (1686, p. 152, pl. 19), which appears to have represented *Balistes capriscus*, and Linnaeus recorded the habitat as "in Europa australi." His record of habitat in 1758 as "ins. Ascensionis" was obviously biased by Osbeck's account. However, excluding those taken from Osbeck, the fin ray counts Linnaeus recorded in both 1754 and 1758 apply to *X. ringens* as we know it, and from his descriptions it seems possible that he had a specimen of this species. If we correctly interpret two of his descriptive terms, they apply to the two or three pigmented grooves under the eye of *X. ringens*—"Balistes lateribus capitis triplicatis" and "Latera capitis plicis 3 mobilibus."

Xanthichthys lineopunctatus (Hollard, 1854), known from South Africa to Mauritius (type locality, Bourbon Island = Reunion), has three to five pigmented grooves below the eye. It is similar to *X. ringens* in having dark spots at the anterior apices of the scales on the ventral third of the body, and these form about six horizontal rows of spots. Scales along the lateral midline of the body have about two rows of spots, elongated into dashes which extend posteriad from the anterior scale apex to about one-third of the scale length. On the upper part of the body these dashes are coalesced to form seven or eight narrow, irregular stripes. This pigmentation was illustrated by Smith (1961, pl. 90, fig. 1165). We have examined two adult *X. lineopunctatus* from South Africa (ANSP 90575, 90648) that appear to have the distinctive pigment pattern described for the type of the species by Hollard (1854).

Xanthichthys mento of the Pacific differs from the other two species in having usually five pigmented grooves below the eye and in not having apical spots on the body scales (see pigment description above).

Thus it appears that there are at least three disjunct populations of *Xanthichthys*, which differ in pigmentation, and which we have recorded as three distinct species. De Beaufort (1962, p. 309) remarked on the great gap in known distribution of *Xanthichthys* between Mauritius (57°46′E.) in the west and Nauru (165°56′E.) in the east. Yet we have seen a small specimen of *Xanthichthys*, which we cannot specifically identify, in the uncataloged USNM collections from the Andaman Sea — nearly in the middle of the hiatus previously thought to exist. Obviously, our current statements on ranges are imperfect, and our conclusions on taxonomy of this genus are tentative.

SYNONYMY. Most citations give the year of publication of Jordan and Gilbert's description of *Balistes mento* as 1881, and pages 225 and 241 (including the description on page 228) have the date December 24, 1881, printed at the bottom. However, Bulletin 193 of the U. S. National Museum, "A list and index of the publications of the United States National Museum (1875–1946)," gave the date of publication of this number as January 4, 1882.

The pigment characters by which we distinguish the three species of *Xanthichthys* develop at about 80 to 140 mm. SL. Without a knowledge of location of capture we cannot identify to species small specimens lacking the specific pigment pattern. Three nominal species in this category predate *X. mento*:

Balistes aureolus Richardson (1844, p. 126, pl. 59, figs. 1–4) is a *Xanthichthys* and has frequently been cited as a synonym of *X. ringens*; however, this is a small specimen of about 58 mm. SL (type in the British Museum of Natural History, according to Günther, 1870, p. 215), and the collection locality is uncertain — Richardson stated, "Sir Edward Belcher did not note the locality in which this fish was taken."

Balistes notatus Gronovius in Gray (1854, p. 36) is a *Xanthichthys* and has been placed in synonymy of *X. ringens* by Jordan and Evermann (1898, p. 1709), who gave the locality of that nominal species as "both Indies." Wheeler (1958, p. 245) listed the holotype of *B. notatus* (BMNH 1853.11.12.188), 133 mm., as a synonym of *X. ringens*, but did not record a type locality.

Balistes heckeli von Müller (1864, p. 182) from "Mexico" has been placed in the synonymy of the Atlantic *X. ringens* (see Jordan and Evermann, 1898, p. 1709), but we have not determined if von Müller's specimen came from the Atlantic or the Pacific coast of Mexico.

Canthidermis maculatus (Bloch).

Ocean Triggerfish, Ocean Turbot, Rough Triggerfish.
(Figures 14, 15, 16.)

Balistes maculatus BLOCH, 1786, vol. 2, p. 25, pl. CLI (type locality, "in den amerikanischen Gewässern").

Balistes americanus GMELIN, 1788, p. 1473 (type locality "in Oceano americano," holotype BMNH 1853.11.12.193, 32 mm. SL, according to Wheeler 1958, p. 245).

Balistes macropterus WALBAUM, 1792, p. 465 (type locality, "in oceano Americano").

Balistes rotundatus PROCÉ, 1822, p. 130 (type locality, "la baie de Manille").

Balistes angulosus QUOY and GAIMARD, 1824, p. 210 (type locality, Sandwich (= Hawaiian) Islands; holotype MNHN B. 1921, 83 mm., 3 paratypes from Hawaiian Islands, New Guinea, and an unknown locality, according to Le Danois 1961, p. 518).

Balistes azureus LESSON, 1830, p. 121, pl. 10, fig. 2 (type locality New Guinea; holotype MNHN B. 1809, 150 mm.; one paratype from Bora-Bora, Society Islands, according to Le Danois 1961, p. 518).

Balistes oculatus GRAY, 1831, vol. 1, pl. 90, fig. 1 (type locality, India; date of publication according to Sawyer, 1953, p. 51).

Balistes willughbeii LAY and BENNETT, 1839, p. 68, pl. XXI, fig. 2 (type locality, Acapulco,

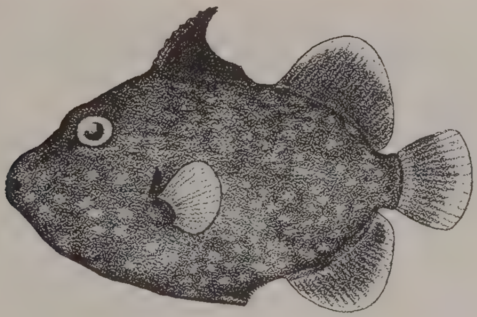

FIGURE 14. *Canthidermis maculatus*, 32 mm. SL, 10 miles S. of Morro Puercas, Panama, UCLA W49-466.

Mexico; counts of softrays low, D. 20, A. 17, but the figure obviously = *C. maculatus*).

Balistes adspersus TSCHUDI, 1845, p. 31 (type locality, Huacho, Peru).

Balistes senticosus RICHARDSON, 1848, p. 23, pl. 9, figs. 5–8 (type locality, Seas of China; holotype in BMNH according to Günther, 1870, p. 215).

Balistes brevissimus HOLLARD, 1854, p. 56, pl. III, fig. 1 (type localities, "Nouvelle-Guinée et l'Australie").

Balistes longissimus HOLLARD, 1854, p. 60, pl. III, fig. 3 (type locality, Vanikoro, Santa Cruz Islands, Society Islands; holotype MNHN B. 1806, 412 mm., according to Le Danois, 1961, p. 519).

Balistes rufus GRONOVIUS in Gray, 1854, p. 36 (type locality, "in Oceano americano," holotype BMNH 1853.11.12.193, 32 mm. SL, according to Wheeler, 1958, p. 245).

Balistes longus GRONOVIUS in Gray, 1854, p. 37 (according to Günther, 1870, p. 214).

Balistes um THIOLLIÈRE, 1857, p. 217 (type locality, Woodlark Island; according to Fowler, 1928, p. 449).

Balistes munumum THIOLLIÈRE, 1857, p. 217 (type locality, Woodlark Island; according to Fowler, 1928, p. 449).

Balistes melanopterus COPE, 1871, p. 478 (type locality, Darien).

Canthidermis viola HERRE, 1926, p. 534, pl. 1 (type locality, Manukan, Cagayan Islands, Sulu Sea).

Canthidermis longirostris TORTONESE, 1954, p. 77, fig. 1 (type locality, "Mar Rosso"; holotype no. 20162 in Dahlak. Mus. Civ. Zoologia, Roma).

Body elongate, becoming more so with increase in size; caudal peduncle compressed; head profile slightly to moderately convex.

Scales covering entire body. No pronounced grooves between scale rows on head or body. Elevations on scales forming slightly irregular ridges on head and body at smaller sizes, these becoming less pronounced and tending to disappear at about 175 mm. SL. No enlarged scales behind gill opening. Incasing scales of pelvis fixed and immovable. Preorbital groove moderately deep and pronounced. Teeth with strong cusps at all sizes, except the two medial teeth of upper jaw tending to lose cusps at about 400 mm.

D. III, 23–25; A. 20–23; P_1 13–15 (table 1). Third spine of dorsal fin

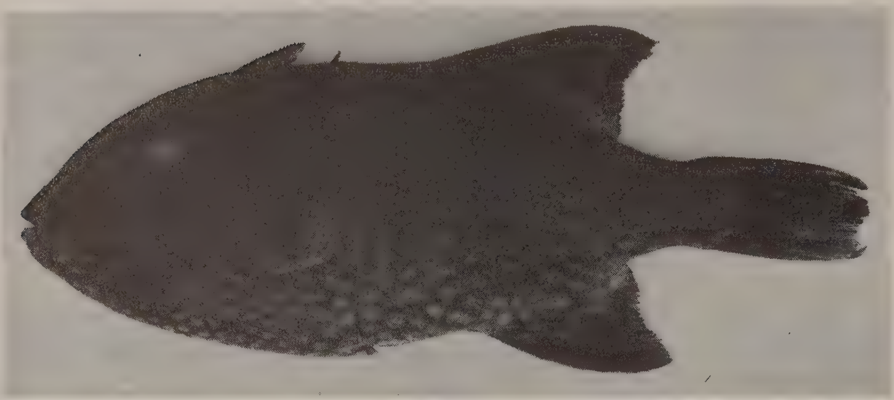

Figure 15. *Canthidermis maculatus*, 161 mm. SL, 150 miles SW. of Acapulco, Mexico, SIO 62-168.

becoming relatively small in larger fish (above about 150 mm. SL); second spine also reduced in very large specimens. Soft dorsal and anal fins becoming falcate in specimens larger than about 110 mm. SL, usually with fourth or fifth dorsal and third or fourth anal rays the longest. Caudal fin rounded at small sizes, becoming biconcave at about 100–150 mm. SL, and the median lobe almost disappearing and the dorsal and ventral lobes pronounced at about 400 mm. SL. Scale rows 36–41 (3 specimens). Gillrakers 24–32 (13 specimens, 45–242 mm.) and about 39 at 482 mm. Vertebrae 7 + 11 (2 specimens).

Pigmentation. Larger juveniles and adults (figs. 15 and 16): Body and head brown, lighter on ventral surfaces, with a number of horizontally elongate spots all over, spots continuing onto dorsal and anal fins and frequently onto caudal fin; the spots less pronounced or missing from some preserved specimens larger than 400 mm. SL (the fins dark brown on these large specimens). Smaller juveniles (fig. 14): Usually with a number of white spots over the body, and a dark first dorsal fin; specimens varying in amount of spotting on soft dorsal and anal fins, and in intensity of dark pigmentation on head and body.

Range. This world-wide species is found inshore in tropical waters, but records indicate that it also inhabits the surface waters of the open ocean without apparent association with land. In the eastern Pacific, it has been recorded from Huacho, Peru (Tschudi, 1845, p. 31, as *B. adspersus*), and we have examined specimens from most of the offshore islands and from Colombia to off central Mexico (fig. 19). It was recorded from numerous Indo-Pacific localities by de Beaufort (1962, p. 311, as *C. rotundatus*).

Relationships. We believe that this oceanic species has a continuous distribution from the eastern Pacific westward to the western Atlantic. We can

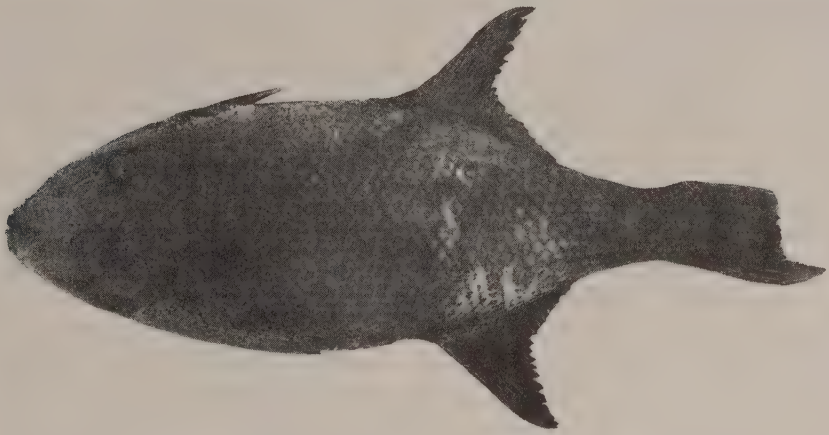

Figure 16. *Canthidermis maculatus*, 482 mm. SL, Clipperton Island, UCLA W56-236.

find no significant differences in large series of specimens from both sides of the American continents. Specimens from various Indo-West-Pacific localities are similar to the American specimens in all respects noted. We are aware of only one other species of *Canthidermis*, *C. sufflamen* (Mitchill) (= *C. sobaco* Poey) of the western Atlantic. This second species has higher numbers of dorsal softrays (25–28) and anal softrays (23–25) — Donald Moore, personal communication.

Synonymy. The synonymy of this species has been confused because identifications and names based on small specimens (as "*rotundatus*" Procé and "*oculatus*" Gray) have not been recognized as conspecific with larger, more elongate specimens (as "*maculatus*" Bloch, "*willughbeii*" Lay and Bennett, and "*longirostris*" Tortonese). As the body length increases, there is a proportionate decrease in head length, eye diameter, body depth, and first dorsal spine length, and a proportionate increase in the lengths of the lobes of the dorsal and anal fins. These relations can be visualized in table 2. This species has usually been identified as "*maculatus*" in the Atlantic, as "*rotundatus*" in the Indo-West-Pacific, and as "*adspersus*," "*rotundatus*," "*angulosus*," or "*maculatus*" in the eastern Pacific.

Specimens Examined

Collection numbers (and pertinent data for uncataloged specimens) from eastern Pacific localities only are listed. Most of these specimens are plotted in figures 17, 18, and 19.

Balistes polylepis (fig. 17). UCLA W49-53, W49-55, W50-24, W50-34, W50-43, W50-188, W51-16, W52-40, W52-45, W53-357, W53-370, W54-366, W55-96, W55-97, W55-122, W55-139, W55-160, W56-111, W56-115, W56-137, W56-276, W56-376, W58-37, W58-46, W58-71, W58-132, W59-13, W60-15, W60-26, W60-97, W60-106. SIO H49-178, H50-79, H50-105, H53-178, 59-281, 60-294, 60-311, 60-355, 60-356, 60-511, 62-18, 62-54, 62-59, 62-65, 62-214, 62-236, 62-703, 62-715, 63-482, 64-63, 64-805, 64-814. LACM W51-108, W59-200, W60-38. ANSP 88972, 88973. CAS 5365, IU13431a, W58-48. SU 6878, 16639, 48174. USNM 165496. BLLJ uncataloged, D5011, 23°00.5′N., 109°34′W., 30 September 1952, stomach contents of *Coryphaena*; S5708, 111G14; Mexico, Magdalena Bay, 28 September 1952; 14°28′N., 92°58′W., 6 February 1962, FB62-186; Ceralbo Island, 29 July 1962, FB62-292; Mexico, Cedros Island, 2 November 1961; D-20, 157.20; 25°37′N., 110°37′W., 17 September 1956; Mexico, 12 miles W. of Magdalena Bay, 18 October 1956; S5708, 153.16; S5708, 99G40; TO-5801-141; S5708, 104G00. BLSD uncataloged, 06°30′N., 82°23′W., 26 April 1963; 09°45′N., 83°37′W., 8 May 1963; 17°22′N., 101°28′W., 16 March 1963.

Pseudobalistes naufragium (fig. 17). UCLA W51-3, W51-43, W51-58, W55-91, W56-114, W56-115, W58-5, W62-63. SIO 62-63. ANSP 77873. BC 59-674. CAS IU13432a. MCZ uncataloged, Panama, Pt. Partilla, 29 April 1962. SU 1656, 6877, 9305. USNM 53485, 65434. BLLJ uncataloged, Mexico, Banderas Bay, 19 August 1961; B6108-31, Mexico, Banderas Bay, 18–19 August 1961.

Sufflamen verres (fig. 18). UCLA W51-43, W51-54, W51-243, W51-252, W51-273, W52-263, W53-126, W53-157, W53-168, W53-293, W53-370, W55-118, W55-161, W56-161, W56-234, W56-235, W56-236, W58-11, W58-37, W58-202, W58-222, W58-287, W58-378, W59-248, W60-139, W60-148, W60-151, W60-176, W61-34. SIO H49-75, H51-61, 58-210, 59-219, 61-237, 61-243, 61-249, 61-250, 61-252, 61-279, 62-20, 62-25, 62-55, 62-58, 62-63, 62-341, 62-726. AHF 2350, 77-61. ANSP 100279. BC 60-464. CAS 6036, 6037, W54-225. MCZ 11872, 36523, 36524. SU 6805, 6905. USNM 47469, 73156. BLLJ uncataloged, B6212-3; Costa Rica, 5 miles SE. of Cabo Blanco, 12 March 1959; Costa Rica, off Cape Velas, September 1959, FB62-253; 11°34.4′N., 87°00′W., FB62-254; Mexico, Cleopha Island, 21–22 August 1961.

Melichthys niger (fig. 18). UCLA W51-266, W53-52, W53-126, W55-52, W55-163, W56-236, W58-378. SIO 59-334, 62-341. ANSP 86278, 89117. BC 54-402, 56-239, 56-361, 56-364, 57-143. CAS 919, 6035. SU 10879, 12338, 12581, 12582. USNM 5988 (locality unknown).

Xanthichthys mento (fig. 19). UCLA W51-92, W51-156, W51-274, W52-81, W52-82, W52-141, W55-123, W55-136, W55-150, W58-281. SIO H49-51, H53-173, 57-72, 57-138, 58-54, 58-139. CAS 1974, 1976, 1977, W53-44, W53-47, W55-127. MCZ 27911, 29374, 29627. SU 6366. USNM 47128, 47129, 47130, 65700. BLLJ uncataloged, H5612, 157.60.

Canthidermis maculatus (fig. 19). UCLA W49-466, W51-266, W53-207,

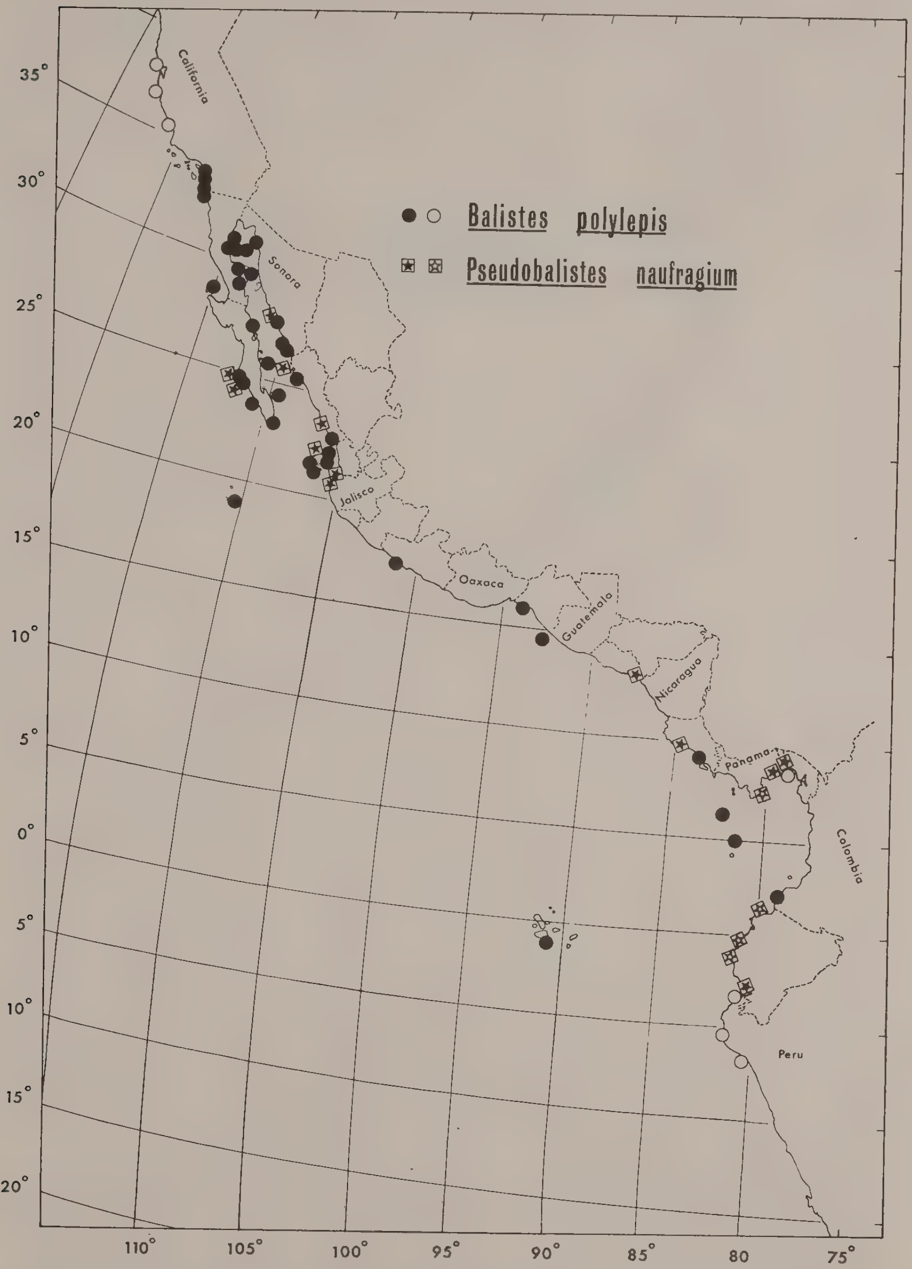
● ○ Balistes polylepis
▣ ▣ Pseudobalistes naufragium
California
Sonora
Jalisco
Oaxaca
Guatemala
Nicaragua
Panama
Colombia
Peru
35°
30°
25°
20°
15°
10°
5°
0°
5°
10°
15°
20°
110°
105°
100°
95°
90°
85°
80
75°

FIGURE 17. *Balistes polylepis* and *Pseudobalistes naufragium* — distribution in the eastern Pacific. Solid symbols represent specimens examined; open symbols represent literature reports. The northernmost record for *B. polylepis* is not shown (41°50′N., 124°22′W.).

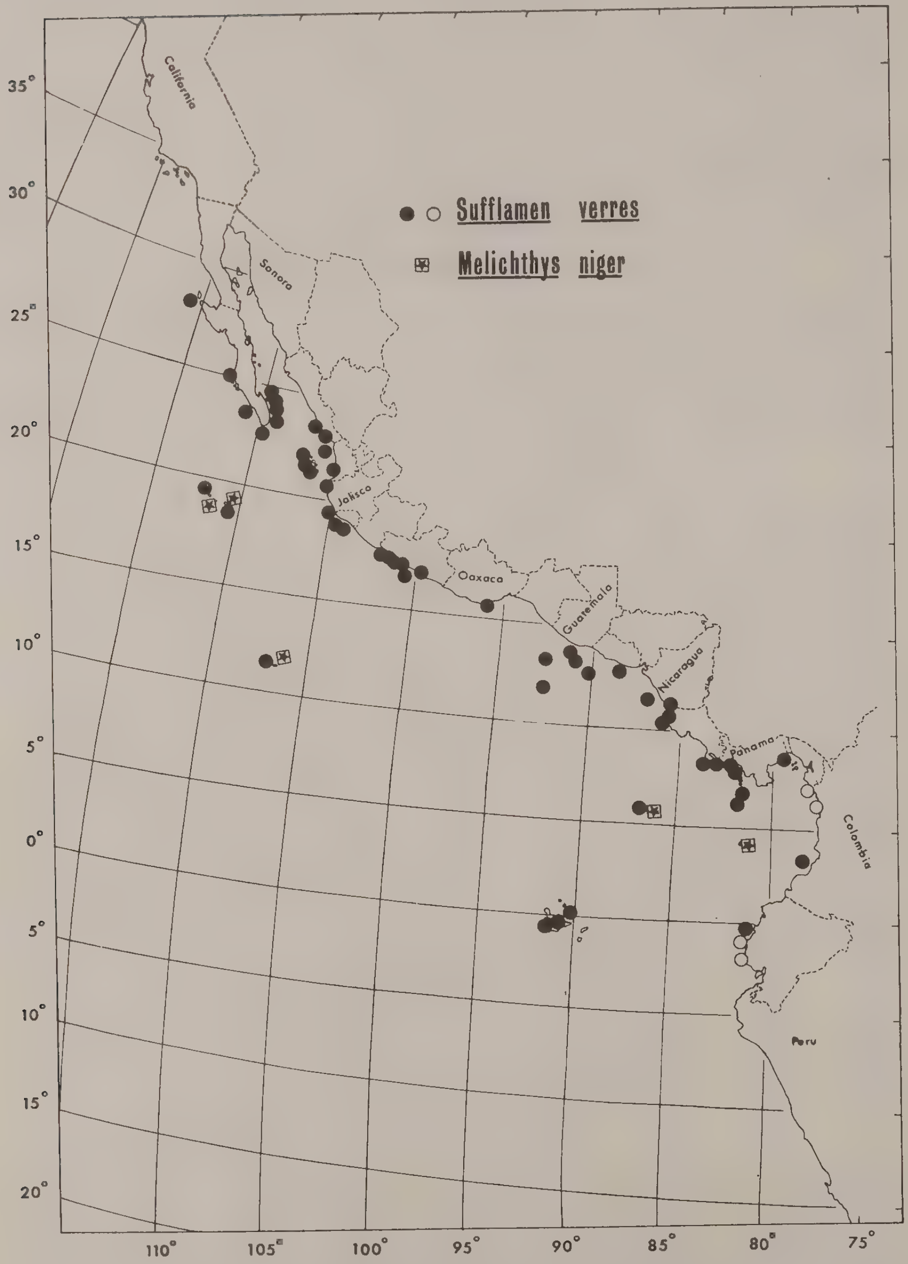
● ○ Sufflamen verres
⊠ Melichthys niger
California
Sonora
Jalisco
Oaxaca
Guatemala
Nicaragua
Panama
Colombia
Peru
35°
30°
25°
20°
15°
10°
5°
0°
5°
10°
15°
20°
110°
105°
100°
95°
90°
85°
80°
75°

FIGURE 18. *Sufflamen verres* and *Melichthys niger*—distribution in the eastern Pacific. Solid symbols represent specimens examined; open symbols represent literature reports.

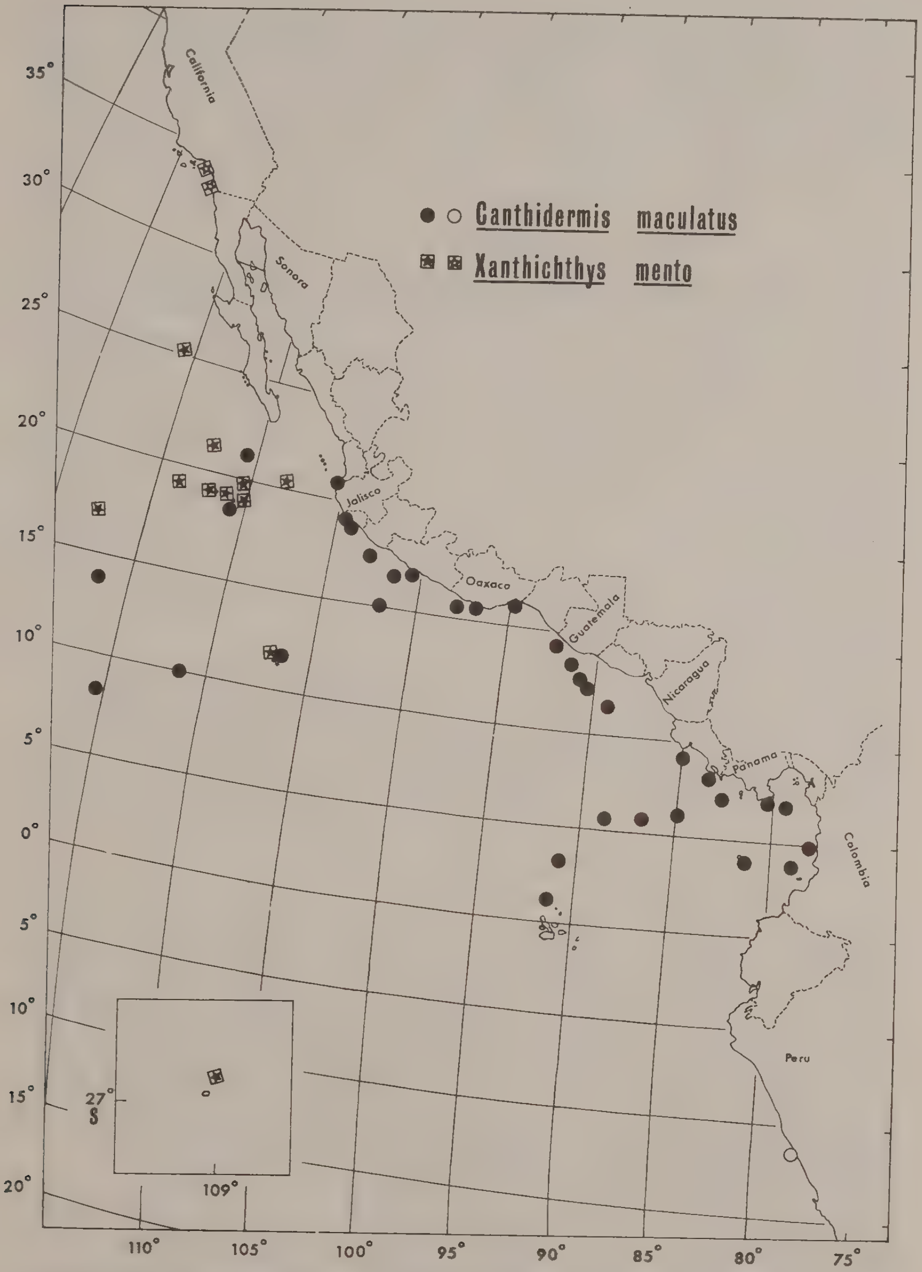
● ○ Canthidermis maculatus
▨ ▨ Xanthichthys mento
California
Sonora
Jalisco
Oaxaca
Guatemala
Nicaragua
Panama
Colombia
Peru
35°
30°
25°
20°
15°
10°
5°
0°
5°
10°
15°
20°
27°
S
109°
110°
105°
100°
95°
90°
85°
80°
75°

FIGURE 19. *Xanthichthys mento* and *Canthidermis maculatus*—distribution in the eastern Pacific. Solid symbols represent specimens examined; open symbols represent literature reports.

W53-299, W53-409, W54-301, W54-302, W54-310, W55-326, W56-12, W56-129, W56-236, W56-330, W57-88, W58-64, W58-213, W58-223, W60-26, W60-132, W60-185, W60-194. SIO H49-75, H52-388, 52-430, 55-227, 55-243, 55-245, 55-247, 57-75, 58-150, 58-153, 58-368, 58-370, 58-375, 58-442, 62-168. BC 56-364. SU 46409. BLLJ uncataloged, Socorro Island, 2 August 1962, FB62-294; 13°29′N., 91°30′W., 2 October 1956; 01°06.2′N., 91°30.7′W.

Synopsis

Balistes polylepis is the most abundant and wide-ranging triggerfish in inshore continental waters of the eastern Pacific. *Sufflamen verres* is probably the next most abundant eastern Pacific balistid, and is more ubiquitous, apparently equally successful as a continental or insular inhabitant. *Pseudobalistes naufragium* is a relatively rare species in tropical continental waters. *Melichthys niger* is primarily an inhabitant of oceanic islands, and may be locally abundant in that environment. *Canthidermis maculatus* is primarily a surface oceanic species that occasionally occurs in inshore waters; it is the most wide-ranging and probably the most abundant, though dispersed, triggerfish in the eastern Pacific. The distribution of *Xanthichthys mento* in the eastern Pacific is not entirely clear; it is often associated with the oceanic islands, and may have an antitropical distribution.

The relationships of the eastern Pacific Balistidae are predominantly with the central and western Pacific Balistidae. With one possible exception in this family, the geminate relationship of species pairs in the eastern Pacific and the western Atlantic, common in many other families of fishes (Jordan, 1908) is lacking. *Balistes polylepis*, obviously related to the Atlantic *B. capriscus*, is more closely related to specimens we have seen from Hawaii. Of the other five species, *Pseudobalistes naufragium* and *Sufflamen verres* are related to species from the central and western Pacific and Indian Oceans which have no representatives in the Atlantic; *Xanthichthys mento* extends across the Pacific and forms a complex with two other species of the Indian and Atlantic Oceans; and *Melichthys niger* and *Canthidermis maculatus* are world-wide or pantropic species. Two species that occur in the western Atlantic, *Balistes vetula* and *Canthidermis sufflamen*, have no counterparts in the eastern Pacific.

A similar zoogeographic arrangement between eastern Pacific and western Atlantic species exists for the filefish family Monacanthidae, according to data of Berry and Vogele (1961) and Randall (1964). There are four species of this family in the eastern Pacific and 10 species in the western Atlantic. *Alutera scripta* (Osbeck) and *Alutera monoceros* (Linnaeus) have world-wide distribution. *Cantherhines dumerili* (Hollard) ranges from the eastern Pacific to the western Indian Ocean and is related to *Cantherhines macrocerus* (Hollard) of the western Atlantic, but no representative of this species complex is known from the eastern Atlantic. *Cantherhines tiki* Randall, an eastern Pacific endemic, is related to *Cantherhines verecundus* Jordan from Hawaii and to *Cantherhines fronticinctus* (Günther) from the western Pacific to the Indian Ocean, but has no Atlantic representative. One species in the western and eastern Atlantic, *Cantherhines pullus* (Ranzani), is related to *Cantherhines pardalis* (Rüppell) from Indian Ocean to French Oceania and to *Cantherhines sandwichiensis* (Quoy and Gaimard) from the Central Pacific, but no representative exists in the eastern Pacific. The remaining six species are endemic to the Atlantic Ocean, and although at least three are closely related to other Indo-Pacific species, none of these is represented in the eastern Pacific — *Alutera schoepfii* (Walbaum), *Alutera heudelotii* Hollard, *Monacanthus tuckeri* Bean, *Monacanthus ciliatus* (Mitchill), *Stephanolepis hispidus* (Linnaeus), and *Stephanolepis setifer* (Bennett). There are no geminate species relationships between the eastern Pacific and the western Atlantic in this family.

Four species of the two families have a world-wide or circumtropical distribution. Of the remaining species, six are eastern Pacific and 12 are western Atlantic. Four of these 18 exist as complexes of two species each with nearly world-wide distribution. In the eastern Pacific, three species are not represented by closely related forms in the western Atlantic, and nine western Atlantic species have no close relatives in the eastern Pacific. Only two species (*B. polylepis* and *B. capriscus*) may have a strict amphi-American relationship, but current uncertainties restrict this evaluation.

In the Balistidae and the Monacanthidae, phylogenetic affinities of eastern Pacific species are closer to the Indo-West-Pacific than to the western Atlantic, and the species composition of the eastern Pacific is relatively depauperate with respect to that of the western Atlantic.

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AGE, LENGTH COMPOSITION, AND CATCH LOCALITIES OF SARDINE LANDINGS ON THE PACIFIC COAST OF THE UNITED STATES AND MEXICO IN 1963–64[1]

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California landings of Pacific sardines, *Sardinops caeruleus* (Girard), during the 1963–64 season amounted to only 2,032 tons, the poorest catch in the history of the fishery. Baja California landings totaled 6,880 tons. Interseason landings for California and Baja California were 1,435 and 11,235 tons, respectively.

Lack of fish in central California caused purse seiners to shift operations to southern California shortly after the opening of the season.

Sardine landings in central California consisted primarily of large, 4- and 5-year-old fish. Southern California landings were dominated by large fish, 4 and 5 years old, with significant quantities of 1- and 2-year-olds at the end of the season. Three-, 4- and 5-year-old fish made up most of the Baja California landings from north of Punta San Pablo.

Sardines were taken close to shore in central California, between Monterey and Point Lopez. Southern California catches were made primarily off the City of San Pedro and Santa Catalina and San Nicholas Islands. Baja California catches were made in three distinct areas: (i) Ensenada south to Punta Soledad, (ii) Cedros Island vicinity, Punta Santa Rosalia south to Punta San Pablo, and (iii) Magdalena Bay.

INTRODUCTION

Each year, since 1941, the California Department of Fish and Game and the U.S. Bureau of Commercial Fisheries have cooperated in the sampling (Figure 1) and age determination of sardine landings. During these years, basic data have been contributed concerning the dynamics of the sardine fishery, commencing with the period of peak abundance in the early 1940's and extending to the low population levels of the 1950's and 1960's.

This report, the 18th of the series, summarizes the length and age composition of the 1963–64 period landings. A discussion of the fishery, economic factors affecting it, and yield per area of the California fishing grounds are also included.

Numerous people are involved in the sampling and scale-reading program. A special acknowledgment is made to Anita E. Daugherty, who retired from the California Department of Fish and Game in early 1964. Miss Daugherty was associated with sardine research for 23 years and made significant contributions to the scale-reading program. The assistance of Robert S. Wolf, U.S. Bureau of Commercial Fisheries, and Harold Hyatt, California Department of Fish and Game, is also gratefully acknowledged. William W. Hatton, California Academy of

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Sciences, did the sampling and contact work with the industry in Baja California. Gertrude Cutler worked on many of the tables and Robert Michaud drew the figures. Appreciation is also extended to the cannery personnel and fishing boat skippers who cooperated with our waterfront representatives.

THE FISHERY

Sardines have declined drastically in numbers and importance over the years, but are still heavily exploited in conjunction with the fishery for jack mackerel (*Trachurus symmetricus*) and Pacific mackerel (*Scomber diego*). Historically, the mackerel fishery in California is a year-around venture, while sardine fishing for the canneries is seasonal. In recent years, the industry in Baja California has taken on added significance by processing a greater portion of the total sardine catch.

The 1963–64 fishing period extended from March 2, 1963, through March 1, 1964. The period consists of an interseason and a season, so age and length data are summarized on this basis. In central California (Point Arguello north), the interseason extended from March 2 through July 31, and the season from August 1 through March 1. In southern California, the season began on September 1, thus extending the interseason in this area through August 31. The season closed for both areas at midnight on March 1, but landings were allowed on March 2.

Landings during the season, sometimes referred to as the cannery season, include both cannery and market deliveries. Market deliveries, used primarily as bait in the San Francisco region striped bass sport fishery, bring a considerably higher price than do sardines sold at the canneries. The special pack privilege was used by one southern California processor during the 1963 interseason. This privilege was designed to

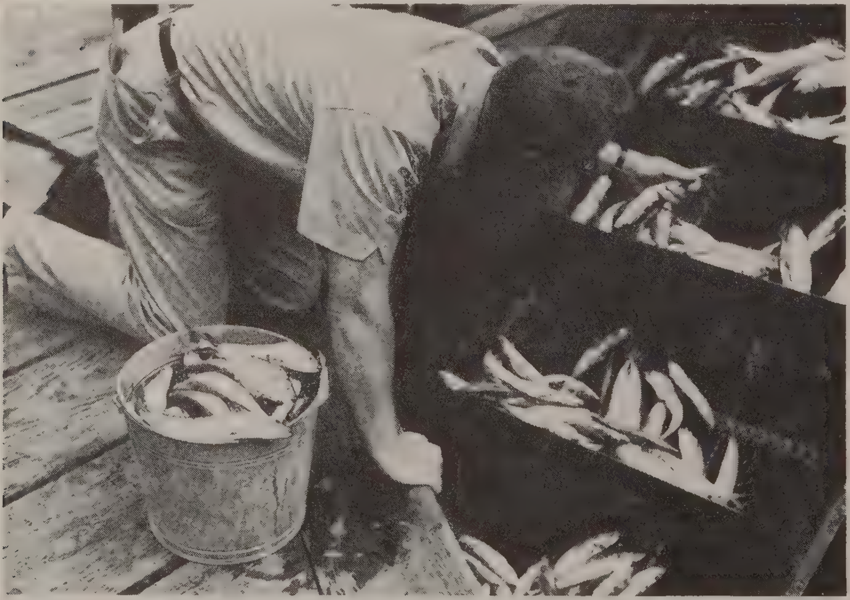

FIGURE 1—Department waterfront representative, Robert Michaud, sampling from a mixed load of mackerel and sardines. *Photograph by Richard Wood, June 1965.*

give canners an opportunity to develop special packs in small cans for competition with imported "sardines". Thus, the southern California interseason landings consisted of both market and cannery deliveries.

For the second consecutive year, California seasonal landings dropped to an all-time low. Central California landings amounted to only 943 tons; southern California landings were only slightly higher at 1,089 tons. Interseason landings for central and southern California were 78 and 1,357 tons respectively, bringing the statewide total to 3,467 tons for the 1963–64 period.

In Baja California, cannery processing is allowed throughout the year, but age and length composition of the 1963–64 landings are summarized on the same interseason and season basis as in southern California. Interseason and season landings were 11,235 and 6,880 tons respectively.

Central California

The season opened on August 1 after all segments of the industry agreed to $60 per ton for sardines and $47.50 for mixed sardines and mackerel. During the last 4 days of the first dark (Table 1), only 107 tons were landed. The second dark, lunar period 542, resulted in the highest catch of the season with 430 tons (Table 9). The majority of this came from Monterey Bay, with the remainder taken off Point Lopez and San Simeon. The balance of the season was unproductive, with fishermen choosing to remain in port rather than fight bad weather and roam far from home searching for fish. The season ended on March 1 with a total of 943 tons landed, the lowest since the prolonged failure of 1952–58.

TABLE 1

Calendar Dates of Lunar Months During 1963–64 Period

Lunar month	Lunar period	Dates
"February"	536*	February 9–March 10
"March"	537	March 11–April 9
"April"	538	April 10–May 8
"May"	539	May 9–June 6
"June"	540	June 7–July 5
"July"	541	July 6–August 4
"August"	542	August 5–September 2
"September"	543	September 3–October 2
"October"	544	October 3–October 31
"November"	545	November 1–November 30
"December"	546	December 1–December 30
"January"	547	December 31–January 28
"February"	548	January 29–February 27
"March"	549†	February 28–March 28

* 1963–64 period began March 2. Lunar months numbered serially since "November" 1919.

† 1963–64 period ended March 1.

During the season, only two plants packed sardines in central California: one at Monterey and one at Moss Landing. A San Francisco plant ceased operations and moved to Oxnard shortly before the season.

Central California fleet operations were unstable, with only five large (60 feet or over) and two small purse seiners operating during the first part of the season. Operations were shifted to southern California in ''September'' and ''October'' due to lack of fish. Thirteen lampara boats operated sporadically throughout the season.

Southern California

The season opened on September 1, but the full-moon period kept boats in port until the evening of September 8. Vessel operators commenced fishing at the price per ton of the previous season, which was in effect in central California. As expected, fishing was poor and only a few small loads of pure sardines were landed. Landings during the first lunar period, ''September'', amounted to only 127 tons (Table 9). ''October'' was only slightly better with 483 tons. Succeeding lunar periods resulted in smaller catches, reaching a low of 17 tons in ''February''. On the last day of the season, March 1, 136 tons were taken from the vicinity of San Nicolas Island. The season catch of 1,089 tons was the smallest in the history of the southern California sardine fishery.

Boat limits, in effect at some canneries, and weather did not materially hold down the catch. Negotiations over the price of mackerel tied the fleet up during January and February.

One cannery processed sardines at Oxnard and five in the Los Angeles area.

Altogether, 70 boats operated in southern California during the season with 34 large purse seiners (60 feet or over) and 29 small purse seiners and lampara boats fishing exclusively in the area. Five large and two small purse seiners from central California entered the southern California fishery shortly after the season opened.

Baja California

Season landings in the Ensenada, Cedros Island, and Puerto Adolfo Lopez Mateos areas amounted to 6,880 tons, and interseason landings to 11,235 tons; the total was about the same as for the 1962–63 period.

Five canneries operated in the Ensenada area, one on Cedros Island, and one at Puerto Adolfo Lopez Mateos. The price to fishermen for sardines varied between $32 and $42 per ton. Economic demand was good and all fish were utilized by the canneries.

Weather conditions were generally favorable throughout the 1963–64 period except off Cedros Island, where poor spring weather reduced landings.

The bulk of sardine catches off northern and central Baja California were made within easy sailing distances from Ensenada and Cedros Island canneries. Substantial tonnages taken in the Cedros Island area were shipped in refrigerated vessels to Ensenada for processing. A thriving fishery for sardines was conducted off southern Baja California. Most of the fish were taken from Magdalena Bay and processed at Puerto Adolfo Lopez Mateos.

AGE AND LENGTH COMPOSITION

Methods of estimating numbers of sardines landed by region and year-class are discussed by Felin and Phillips (1948, p. 11).

During the season 650 fish were measured in central California, 900 in southern California, 850 in northern Baja California, and 650 in

TABLE 2

Length Composition of Year-classes in Sardine Samples from the Central California Commercial Catch, 1963–64 Season

Standard length (mm)	Year-class							Totals	
	1962	1961	1960	1959	1958	1957	1956	Aged	Measured
150	--	--	--	--	--	--	--	--	--
152	--	--	--	--	--	--	--	--	--
154	--	--	--	--	--	--	--	--	--
156	--	--	--	--	--	--	--	--	--
158	--	1	--	--	--	--	--	1	1
160	--	--	--	--	--	--	--	--	1
162	--	--	--	--	--	--	--	--	1
164	--	2	1	--	--	--	--	3	6
166	--	--	--	--	--	--	--	--	2
168	--	1	--	--	--	--	--	1	2
170	--	--	--	--	--	--	--	--	3
172	--	1	--	--	--	--	--	1	3
174	--	1	--	--	--	--	--	1	6
176	--	1	--	--	--	--	--	1	2
178	--	--	--	--	--	--	--	--	--
180	--	--	--	--	--	--	--	--	1
182	--	--	--	--	--	--	--	--	--
184	--	--	--	--	--	--	--	--	1
186	--	--	--	--	--	--	--	--	2
188	--	--	--	--	--	--	--	--	1
190	--	--	--	--	--	--	--	--	--
192	--	--	--	--	--	--	--	--	1
194	--	--	--	--	--	--	--	--	--
196	--	--	--	--	--	--	--	--	2
198	--	--	--	--	--	--	--	--	--
200	--	--	--	--	--	--	--	--	--
202	--	--	--	--	--	--	--	--	3
204	--	--	--	--	--	--	--	--	--
206	--	--	1	--	--	--	--	1	2
208	--	1	--	1	--	--	--	2	4
210	--	--	--	--	--	--	--	--	1
212	--	--	--	--	--	--	--	--	3
214	--	1	--	--	--	--	--	1	3
216	--	--	--	--	--	--	--	--	3
218	--	--	--	--	--	--	--	--	4
220	--	--	--	--	--	--	--	--	5
222	--	--	--	--	--	--	--	--	3
224	--	--	--	--	--	--	--	--	1
226	--	--	1	--	--	--	--	1	3
228	--	--	--	--	--	--	--	--	3
230	--	--	--	--	1	1	--	2	6
232	--	--	--	--	1	--	--	1	9
234	--	--	--	--	1	--	--	1	15
236	--	--	--	1	4	2	--	7	23
238	--	--	1	--	1	--	--	2	17

TABLE 2—Continued

Length Composition of Year-classes in Sardine Samples from the Central California Commercial Catch, 1963–64 Season—Continued

Standard length (mm)	Year-class							Totals	
	1962	1961	1960	1959	1958	1957	1956	Aged	Meas ured-
240	--	--	1	3	2	--	--	6	23
242	--	--	--	1	1	2	--	4	33
244	--	--	1	4	8	1	--	14	49
246	--	--	2	4	6	1	1	14	54
248	--	--	--	3	3	3	2	11	64
250	--	--	--	3	6	--	--	9	55
252	--	--	1	1	1	1	--	4	46
254	--	--	--	2	8	--	--	10	47
256	--	--	--	1	5	2	--	8	35
258	--	--	--	1	3	1	--	5	28
260	--	--	--	1	3	--	1	5	24
262	--	--	--	3	2	--	1	6	21
264	--	--	--	--	1	--	--	1	11
266	--	--	--	1	1	1	--	3	4
268	--	--	--	--	1	--	--	1	3
270	--	--	--	--	--	--	--	--	4
272	--	--	--	--	--	--	--	--	4
274	--	--	--	--	--	--	--	--	--
276	--	--	--	--	--	--	--	--	1
278	--	--	--	--	--	--	--	--	--
280	--	--	--	--	--	--	--	--	1
Totals	--	9	9	30	59	15	5	127	650
Mean lengths	--	178	229	248	249	247	253	243	243

TABLE 3

Length Composition of Year-classes in Sardine Samples from the Southern California Commercial Catch, 1963–64 Season

Standard length (mm)	Year-class							Totals	
	1962	1961	1960	1959	1958	1957	1956	Aged	Measured
168	--	--	--	--	--	--	--	--	2
170	--	1	--	--	--	--	--	1	7
172	1	--	--	--	--	--	--	1	6
174	--	--	--	--	--	--	--	--	7
176	1	1	--	--	--	--	--	2	6
178	1	--	--	--	--	--	--	1	6
180	--	1	--	--	--	--	--	1	3
182	--	1	--	--	--	--	--	1	7
184	--	2	--	--	--	--	--	2	3
186	--	1	--	--	--	--	--	1	3
188	--	--	--	--	--	--	--	--	--
190	--	--	--	--	--	--	--	--	--
192	--	--	--	--	--	--	--	--	1
194	--	--	--	--	--	--	--	--	--
196	--	--	--	--	--	--	--	--	1

TABLE 3—Continued

Length Composition of Year-classes in Sardine Samples from the Southern California Commercial Catch, 1963–64 Season—Continued

Standard length (mm)	Year-class							Totals	
	1962	1961	1960	1959	1958	1957	1956	Aged	Measured
198	--	--	--	--	--	--	--	--	3
200	--	1	--	--	--	--	--	1	7
202	--	--	--	--	--	--	--	--	1
204	--	--	1	--	--	--	--	1	6
206	--	--	--	--	--	--	--	--	8
208	--	--	1	--	--	--	--	1	5
210	--	1	--	--	--	--	--	1	6
212	--	--	1	--	--	--	--	1	5
214	--	--	--	1	--	--	--	1	6
216	--	--	--	--	--	--	--	--	5
218	--	--	--	--	--	--	--	--	4
220	--	--	--	1	--	--	--	1	3
222	--	--	--	3	1	--	--	4	6
224	--	--	--	1	1	1	--	3	11
226	--	--	1	2	1	--	--	4	18
228	--	--		--	2	--	--	4	25
230	--	--		2	1	--	--	4	26
232	--	--		9	2	1	--	14	58
234	--	--	2	6	2	--	--	10	59
236	--	--	--	7	8	2	--	17	66
238	--	--	1	6	3	1	1	12	76
240	--	--	2	9	2	1	--	14	71
242	--	--	1	5	5	2	--	13	68
244	--	--	--	5	4	--	--	9	68
246	--	--	4	6	5	--	--	15	47
248	--	--	1	2	3	1	1	8	52
250	--	--	1	2	3	5	--	11	52
252	--	--	--	2	2	--	--	4	28
254	--	--	--	2	1	1	--	4	19
256	--	--	--	--	--	--	--	--	14
258	--	--	--	--	1	--	--	1	14
260	--	--	--	--	1	--	--	1	5
262	--	--	--	1	--	--	--	1	4
264	--	--	--	--	--	--	--	--	--
266	--	--	--	--	--	--	--	--	1
268	--	--	--	--	--	--	--	--	--
270	--	--	--	--	--	--	--	--	1
Totals	3	9	21	72	48	15	2	170	900
Mean lengths	175	186	234	238	241	243	243	235	235

central Baja California (Tables 2–5). The average weights[2] of sardines taken from these areas were: central California 0.4476 pounds, southern California 0.3120 pounds, northern Baja California (Ense-

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[2] Determined by dividing total seasonal catch in pounds by total estimated number of sardines.

TABLE 4

Length Composition of Year-classes in Sardine Samples from the Northern Baja California Commercial Catch, 1963–64 Season

Standard length (mm)	Year-class							Totals	
	1962	1961	1960	1959	1958	1957	1956	Aged	Measured
184	--	--	--	--	--	--	--	--	1
186	--	--	--	--	--	--	--	--	4
188	--	--	--	--	--	--	--	--	--
190	--	--	--	--	--	--	--	--	--
192	--	--	1	--	1	--	--	2	8
194	--	--	3	--	--	--	--	3	13
196	--	--	1	2	--	--	--	3	12
198	--	--	1	1	--	--	--	2	22
200	--	--	2	1	--	1	--	4	19
202	--	--	--	--	1	--	--	1	22
204	--	--	--	1	2	--	--	3	27
206	--	--	2	3	--	--	--	5	33
208	--	--	--	1	2	--	--	3	27
210	--	--	--	2	--	2	2	6	34
212	--	--	1	2	1	--	--	4	27
214	--	--	1	3	1	--	--	5	42
216	--	--	2	3	2	--	1	8	35
218	--	--	--	4	2	--	--	6	55
220	--	--	2	6	4	2	--	14	53
222	--	--	1	2	4	--	--	7	52
224	--	--	1	3	1	1	--	6	43
226	--	--	1	7	4	--	--	12	55
228	--	--	1	5	4	1	--	11	46
230	--	--	--	6	3	1	--	10	38
232	--	--	3	6	3	--	--	12	62
234	--	--	1	4	3	--	--	8	40
236	--	--	--	4	1	--	--	5	21
238	--	--	1	2	4	--	--	7	17
240	--	--	--	2	--	--	--	2	12
242	--	--	--	3	1	--	--	4	12
244	--	--	--	--	--	--	--	--	5
246	--	--	--	1	--	--	--	1	2
248	--	--	--	--	--	--	--	--	1
250	--	--	--	--	--	--	--	--	1
252	--	--	--	--	--	--	--	--	2
254	--	--	--	--	--	--	--	--	--
256	--	--	--	--	--	--	--	--	--
258	--	--	--	--	1	--	--	1	1
Totals	--	--	25	74	45	8	3	155	850
Mean lengths	--	--	214	224	224	218	212	222	219

nada) 0.3389 pounds, and central Baja California (Cedros Island) 0.2233 pounds.

In central California, sardines sampled ranged from 158 mm to 280 mm SL with a mean of 243 mm. The 1958 year-class (5-year-olds) dominated the central California catch, comprising 50 percent of the

TABLE 5

Length Composition of Year-classes in Sardine Samples from the Central Baja California Commercial Catch, 1963–64 Season

Standard length (mm)	Year-class						Totals	
	1962	1961	1960	1959	1958	1957	Aged	Measured
160	--	--	--	--	--	--	--	3
162	--	--	--	--	--	--	--	2
164	--	--	--	--	--	--	--	--
166	--	--	--	--	--	--	--	3
168	--	--	--	--	--	--	--	1
170	--	1	--	1	--	--	2	6
172	--	1	2	--	--	--	3	12
174	--	--	--	4	--	--	4	22
176	--	--	1	--	--	--	1	18
178	--	--	--	1	--	--	1	18
180	--	1	4	2	1	--	8	27
182	--	--	4	3	1	--	8	44
184	--	1	3	3	--	--	7	54
186	--	--	9	3	--	1	13	51
188	--	--	8	10	1	--	19	75
190	--	1	6	6	3	--	16	67
192	--	--	5	6	1	--	12	69
194	--	--	5	7	2	--	14	67
196	--	--	3	2	2	1	8	38
198	--	--	3	5	--	--	8	37
200	--	--	3	1	--	--	4	16
202	--	--	--	1	--	--	1	7
204	--	--	--	--	--	--	--	5
206	--	--	--	--	1	--	1	4
208	--	--	--	--	--	--	--	4
210	--	--	--	--	--	--	--	--
Totals	--	5	56	55	12	2	130	650
Mean lengths	--	179	188	189	192	191	188	188

numbers landed (Table 9, Figure 2). This year-class dominated the landings of the previous season as 4-year-olds. Since the 1961–62 season, central California landings have consisted primarily of large fish, 4, 5, and 6 years old. Two-year-olds have not contributed significantly to the fishery since the 1958–59 season, the year of sardine resurgence in central California.

Lengths of sardines sampled in southern California ranged from 168 to 270 mm with a mean of 235 mm. The 1958 and 1959 year-classes were dominant and contributed over 50 percent of the numbers caught (Table 9, Figure 2). The 1961 and 1962 year-classes, on the strength of catches from San Nicolas Island on the last day of the season, accounted for 28 percent of the landings.

Sardine fishing for Baja California canneries is not restricted to any one time of the year. For comparative purposes, the data have been

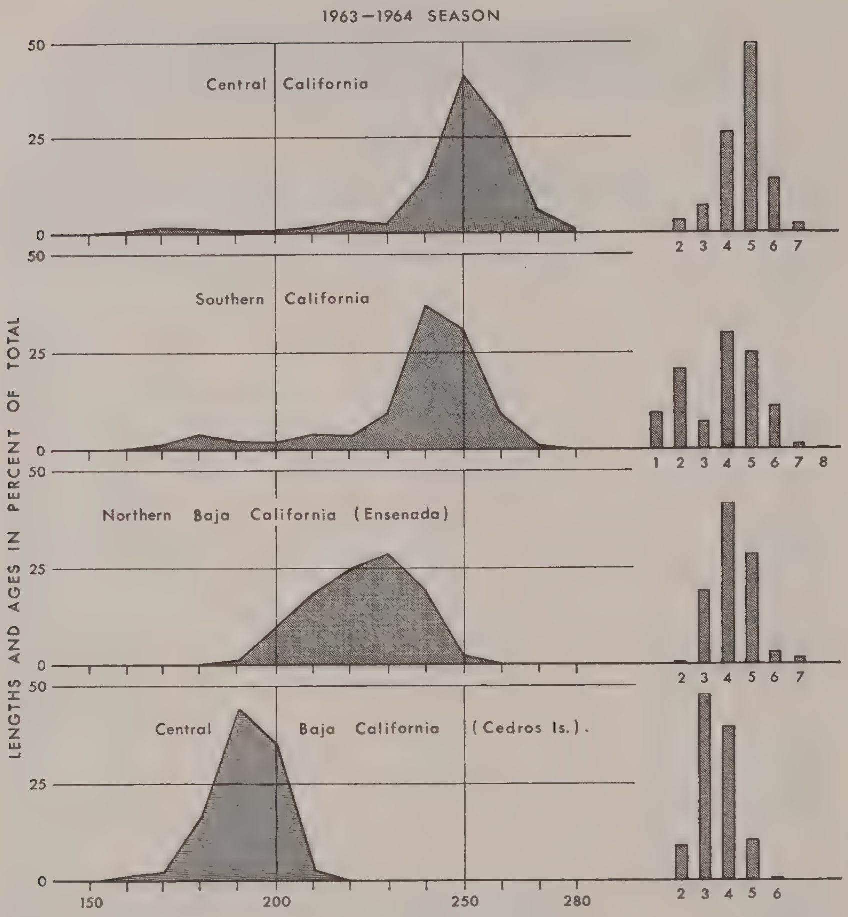


FIGURE 2—Length and age composition of 1963–64 sardine catch. Lengths are plotted by 10mm intervals and by percentage of total numbers sampled. Ages plotted by percentage of estimated numbers landed.

summarized on the same basis as those for southern California. During the 1963–64 season, sardines sampled from Baja California were smaller than those from central and southern California (Figure 2). Historically, sardines from Baja California are much smaller per given age and investigators have allied this with serological differences to substantiate the subpopulation theory (Vrooman, 1964).

The lengths of sardines in northern Baja California samples ranged from 184 to 258 mm with a mean of 219 mm. Fish from central Baja California were considerably smaller, ranging from 160 to 208 mm with a mean of 188 mm (Tables 4 and 5). The 1958 and 1959 year-classes (ages 5 and 4) were major contributors to the catch in northern Baja California (Figure 2). In central Baja California, the 1959 and 1960 year-classes were dominant.

TABLE 6

Length Composition of Year-classes in Sardine Samples from the Southern California Interseason Catch, 1963 (April and May)

Standard length (mm)	Year-class							Totals	
	1962	1961	1960	1959	1958	1957	1956	Aged	Measured
210	--	--	--	--	--	--	--	--	1
212	--	--	--	--	--	--	--	--	--
214	--	--	--	--	--	--	--	--	--
216	--	--	--	--	--	--	--	--	1
218	--	--	--	1	--	--	--	1	2
220	--	--	--	--	--	--	--	--	3
222	--	--	--	--	--	--	--	--	1
224	--	--	--	--	--	--	--	--	3
226	--	--	--	--	--	--	--	--	3
228	--	--	--	--	--	--	--	--	4
230	--	--	--	2	1	--	--	3	9
232	--	--	--	--	1	--	--	1	11
234	--	--	--	--	--	--	--	--	8
236	--	--	1	2	3	1	--	7	13
238	--	--	--	1	1	--	--	2	9
240	--	--	--	1	--	--	--	1	11
242	--	--	1	--	1	--	--	2	10
244	--	--	--	3	1	--	1	5	14
246	--	--	--	1	3	--	1	5	11
248	--	--	--	--	--	--	--	--	4
250	--	--	--	--	--	--	--	--	2
252	--	--	--	--	--	--	--	--	3
254	--	--	--	--	1	--	--	1	2
256	--	--	--	--	--	--	--	--	1
258	--	--	--	--	--	--	--	--	--
260	--	--	--	--	1	1	--	2	2
262	--	--	--	--	--	--	--	--	--
264	--	--	--	--	--	--	--	--	1
Totals	--	--	2	11	13	2	2	30	129
Mean lengths	--	--	239	237	242	248	245	241	238

Interseason landings in central California were negligible and adequate samples were not obtained. Southern California interseason landings were sampled during April and May. Fish varied between 210 and 264 mm and consisted primarily of the 1958 and 1959 year-classes (Table 6). These year-classes also dominated catches during the season.

Sardines sampled from northern Baja California interseason catches ranged in length from 156 to 246 mm with a mean of 213 mm (Table 7). Central Baja California sardines ranged in length from 136 to 204 mm and averaged 180 mm (Table 8). In northern and central Baja California the 1959 and 1960 year-classes were dominant, contributing 81 percent of the total numbers landed (Table 10).

TABLE 7

Length Composition of Year-classes in Sardine Samples from the Northern Baja California Inter-season Catch, 1963

Standard length (mm)	Year-class						Totals	
	1962	1961	1960	1959	1958	1957	Aged	Measured
156	--	--	--	--	--	--	--	2
158	--	--	--	--	--	--	--	1
160	--	--	--	--	--	--	--	3
162	--	--	--	--	--	--	--	2
164	--	--	--	--	--	--	--	--
166	--	--	--	--	--	--	--	--
168	1	--	--	--	--	--	1	2
170	--	--	--	--	--	--	--	--
172	--	1	--	--	--	--	1	2
174	--	--	--	--	--	--	--	6
176	--	--	--	--	--	--	--	6
178	--	1	--	--	--	--	1	2
180	--	--	--	--	--	--	--	3
182	--	1	--	--	--	--	1	1
184	--	--	--	--	--	--	--	1
186	--	--	--	--	--	--	--	3
188	--	--	--	--	--	--	--	4
190	1	--	--	1	--	--	2	11
192	--	--	--	--	--	--	--	12
194	--	1	1	--	1	--	3	19
196	--	--	2	1	--	--	3	17
198	1	--	1	--	--	1	3	27
200	--	--	3	4	1	--	8	40
202	--	--	3	2	1	--	6	41
204	--	--	2	3	2	1	8	66
206	--	--	4	2	3	1	10	48
208	--	1	3	5	1	--	10	63
210	--	--	4	6	2	--	12	78
212	--	--	8	5	3	--	16	55
214	--	--	5	7	1	--	13	92
216	--	--	9	7	3	1	20	70
218	--	--	6	8	4	--	18	70
220	--	--	5	7	3	--	15	70
222	--	--	5	7	--	--	12	74
224	--	--	3	7	3	--	13	60
226	--	--	1	7	2	--	10	38
228	--	--	5	4	3	--	12	40
230	--	--	4	1	2	--	7	34
232	--	--	2	5	2	--	9	26
234	--	--	--	2	1	--	3	17
236	--	--	--	--	1	--	1	11
238	--	--	--	1	3	1	5	12
240	--	--	--	2	--	--	2	8
242	--	--	1	1	--	--	2	3
244	--	--	--	--	--	--	--	2
246	--	--	--	--	--	--	--	1
248	--	--	--	--	--	--	--	--
250	--	--	--	--	--	--	--	--
Totals	3	5	77	95	42	5	227	1,143
Mean lengths	185	187	215	218	219	212	216	213

TABLE 8

Length Composition of Year-classes in Sardine Samples from Central Baja California Interseason Catch, 1963

Standard length (mm)	Year-class						Totals	
	1962	1961	1960	1959	1958	1957	Aged	Measured
136	--	--	--	--	--	--	--	1
138	--	--	--	--	--	--	--	1
140	--	--	--	--	--	--	--	--
142	--	--	--	--	--	--	--	1
144	--	--	--	--	--	--	--	1
146	--	--	--	--	--	--	--	1
148	--	--	--	--	--	--	--	2
150	--	--	--	--	--	--	--	--
152	--	--	--	--	--	--	--	9
154	--	--	--	--	--	--	--	8
156	--	--	--	--	--	--	--	5
158	--	1	1	--	--	--	2	19
160	--	--	2	--	--	--	2	12
162	--	--	--	--	--	--	--	4
164	--	--	1	--	--	--	1	9
166	--	--	1	--	--	--	1	13
168	--	--	3	--	--	--	3	20
170	--	--	2	3	--	--	5	23
172	--	1	4	2	--	--	7	49
174	--	--	2	5	2	--	9	54
176	--	--	5	8	2	1	16	69
178	--	--	9	12	3	--	24	103
180	--	2	8	4	4	--	18	91
182	--	1	13	3	--	--	17	86
184	--	5	13	4	1	--	23	112
186	--	1	4	6	1	1	13	68
188	--	1	5	2	2	--	10	51
190	--	1	4	2	--	--	7	43
192	--	--	6	4	2	--	12	43
194	--	1	2	1	--	--	4	16
196	--	--	1	3	1	1	6	12
198	--	--	4	1	--	--	5	18
200	--	--	--	--	--	--	--	2
202	--	--	--	--	--	--	--	2
204	--	--	--	--	--	--	--	3
Totals	--	14	90	60	18	3	185	953
Mean lengths	--	182	182	182	182	186	182	180

TABLE 9

Age and Year-class Composition of the Sardine Catch in the 1963–64 Season

	Catch		Number of fish in thousands by age and year-class							
	Tons	Number	1 1962	2 1961	3 1960	4 1959	5 1958	6 1957	7 1956	8 1955
Central California										
"July"*	107	476	--	--	--	67	409			
"August"	430	1,780	--	53	214	623	730	160		
"September"	167	884	--	62	53	141	407	177	44	
"October"	9	41	--	12	5	4	18	2		
"November"	Trace									
"December"	37	202	--	--	16	41	85	48	12	
"January"	44	187	--	--	11	7	79	64	26	
"February"	149	640	--	--	--	173	365	102		
Total Central California	**943**	**4,210**	--	**127**	**299**	**1,056**	**2,093**	**553**	**82**	
Percent	--	100.00	--	3.02	7.10	25.08	49.71	13.14	1.95	
Southern California										
"September"	127	688	--	14	191	287	165	20	9	2
"October"	483	2,599	--	104	208	987	738	520	42	
"November"	185	928	--	--	6	353	439	105	25	
"December"	101	577	--	--	--	277	254	46		
"January"†	40	229	--	--	25	89	106	9		
"February"	17	94	--	--	21	28	45			
"March"‡	136	1,868	635	1,233						
Total Southern California	**1,089**	**6,983**	**635**	**1,351**	**451**	**2,021**	**1,747**	**700**	**76**	**2**
Percent	--	100.00	9.09	19.35	6.46	28.94	25.02	10.02	1.09	0.03
Total California	2,032	11,193	635	1,478	750	3,077	3,840	1,253	158	2
Percent	--	100.00	5.67	13.20	6.70	27.49	34.31	11.20	1.41	0.02
Baja California§										
"September"	957	6,950	--	--	1,736	3,554	1,316	239	105	
"October"	931	6,607	--	435	1,686	2,875	1,277	197	137	
"November"	1,166	8,367	--	660	3,249	3,749	532	113	64	
"December"	1,034	7,872	--	128	2,707	3,504	1,321	212		
"January"	884	7,323	--	76	3,732	2,104	1,411			
"February"	357	2,865	--	37	1,453	814	561			
"March"										
Total Baja California	**5,329**	**39,984**	--	**1,336**	**14,563**	**16,600**	**6,418**	**761**	**306**	
Percent	--	100.00	--	3.34	36.42	41.52	16.05	1.90	0.77	

* August 1–4

† No samples, Dec. and Feb. sampling used.

‡ Feb. 28–March 2 landings

§ Includes Cedros Island and Ensenada only—1,551 tons from southern Baja cannery not sampled.

TABLE 10

Age and Year-class Composition of the Sardine Catch in the 1963 Baja California Interseason

	Catch		Numbers of fish in thousands by age and year-class						
	Tons	Number	1 1962	2 1961	3 1960	4 1959	5 1958	6 1957	7 1956
Baja California*									
"February"†	204	1,776	1	290	957	334	112	82	
"March"	872	7,160	4	957	3,836	1,514	543	306	
"April"	963	7,430	--	1,134	3,722	1,893	645	36	
"May"	1,070	8,416	76	305	3,350	3,611	987	87	
"June"	1,573	11,358	--	393	4,014	6,090	861		
"July"	1,159	10,060	32	1,053	5,224	2,510	1,097	144	
"August"‡	870	6,281	--	--	1,892	3,739	457	193	
Total	**6,711**	**52,481**	**113**	**4,132**	**22,995**	**19,691**	**4,702**	**848**	
Percent	--	100.00	0.22	7.87	43.82	37.52	8.96	1.62	

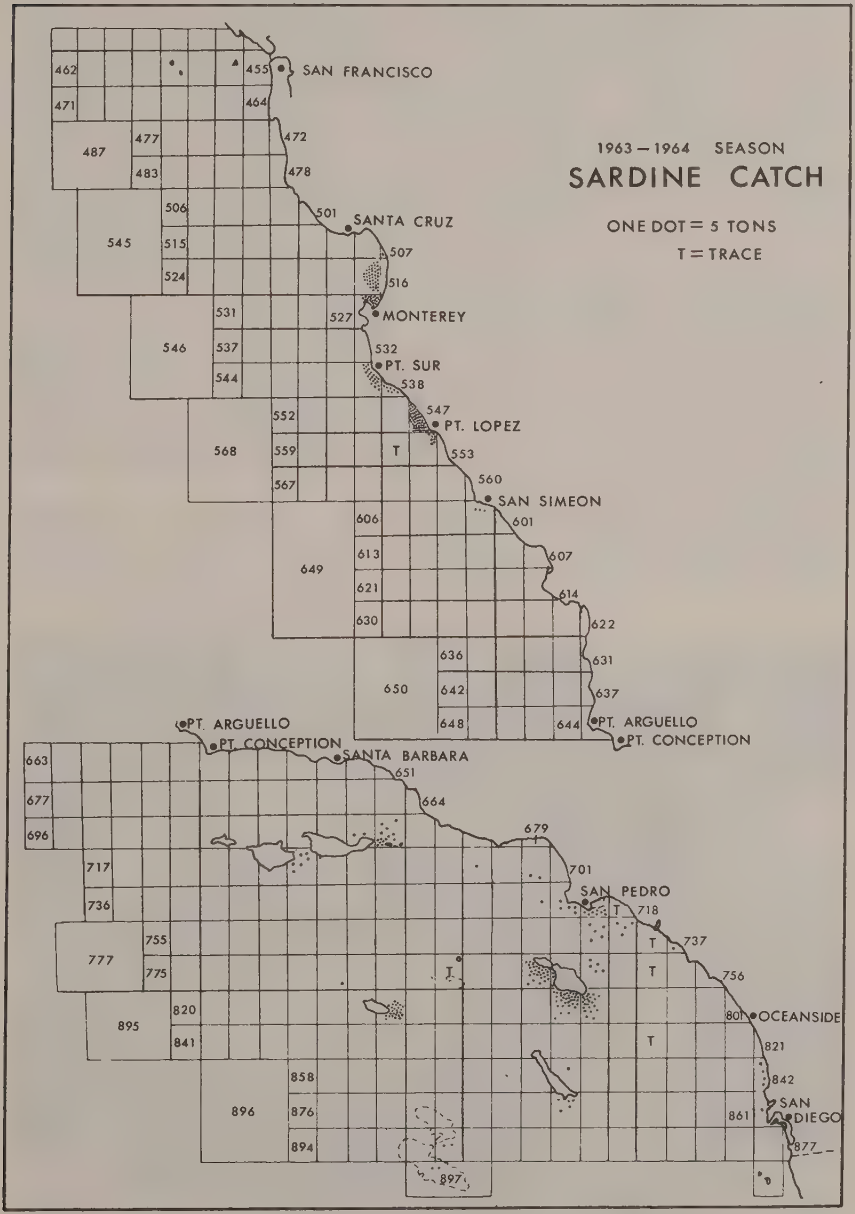
* Includes Cedros Island and Ensenada only—4,524 tons from southern Baja California cannery not sampled.

† March 3–10, no samples, "March" used.

‡ September 1–2, no fish landed

Catch Localities

Areas of catch are important to the fisheries scientist interested in the relationships of the fish to its environment. The population dynamicist is interested in major shifts of catch areas that may be related to en-


1963 – 1964 SEASON
SARDINE CATCH
ONE DOT = 5 TONS
T = TRACE
SAN FRANCISCO
SANTA CRUZ
MONTEREY
PT. SUR
PT. LOPEZ
SAN SIMEON
PT. ARGUELLO
PT. CONCEPTION
SANTA BARBARA
SAN PEDRO
OCEANSIDE
SAN DIEGO
462
471
455
464
472
487
477
483
478
501
506
545
515
524
507
516
531
527
546
537
544
532
538
552
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560
606
601
613
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649
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696
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717
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736
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718
755
T
737
777
T
775
T
756
820
801
895
841
T
821
858
842
896
876
861
894
877
897

FIGURE 3—Sardine catch origins 1963–64 season. Dots are placed in approximate locations, relative to land masses where fish are known to have been taken.

vironmental changes resulting in displacement of subpopulations into areas of different fishing pressure. Past reports on yield per area (California State Fisheries Laboratory, 1930; Clark, 1937 a, b; Pinkas, 1951; Clothier and Greenhood, 1956) covered the fishery during its inception, rapid expansion, and decline in the early 1950's.

The data for this report are derived from the California pink ticket system, which has been well documented (California Bureau of Marine Fisheries, 1952) and consists of fish receipts (pink) filled in by the dealer at the time he purchases fish from the fishermen. The tickets list the variety of fish, pounds landed, and block area of catch. Block areas are 10 minutes of latitude by 10 minutes of longitude (Figure 3). At times, dealers do not enter the catch areas, but during the sardine season ''checkers'' are employed by the Department to interview the vessel captain at time of unloading and insure that all data concerning each catch are on a special checker's ticket. The system is also supplemented by scientific personnel who interview the vessel captains when sampling sardine catches (Figure 4).

The 1963–64 season catch localities off California consisted of three major areas: the central California coast from Monterey Bay to Point Lopez; the southern California coastal area off San Pedro; and the offshore islands of southern California (Figure 3). The catch origins correspond quite well to an early analysis by Clark (1937), in which most fish were taken within 3–5 miles of shore and in areas shallower than 500 fathoms.

To examine major shifts in areas of catch, tonnages for individual blocks have been grouped into general fishing areas (Table 11). Season and interseason tonnages were computed, and the tonnage of each gen-

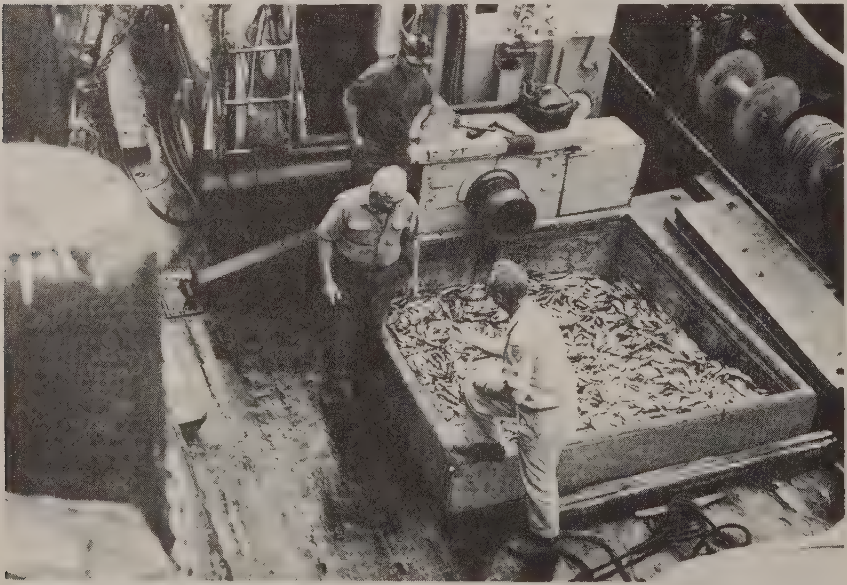

FIGURE 4—Vessel personnel being interviewed on the activities of their vessel during the previous night of fishing. *Photograph by Richard Wood, June 1965.*

TABLE 11

Sardine Catch by General Fishing Areas for 1963–1964 Period

General areas	Block numbers	Interseason*		Season†		Total	
		Pounds	Percent	Pounds	Percent	Pounds	Percent
Point Arena	401–421	--	0.0	--	0.0	--	0.0
Bodega Head	422–445	--	0.0	--	0.0	--	0.0
San Francisco	446–471	--	0.0	--	0.0	--	0.0
Pigeon Point	472–506	--	0.0	--	0.0	--	0.0
Monterey	507–531	71,819	2.5	668,938	16.5	740,757	10.7
Point Sur	532–552	--	0.0	843,725	20.8	843,725	12.2
Piedras Blancas	553–606	--	0.0	123,420	3.0	123,420	1.8
Point Buchon	607–630	--	0.0	--	0.0	--	0.0
Point Sal	631–648	--	0.0	--	0.0	--	0.0
Santa Barbara	651–657, 665–671	--	0.0	--	0.0	--	0.0
Port Hueneme	664, 680–683, 703–706, 722–725	62,600	2.2	5,950	0.1	68,550	1.0
Santa Cruz Island	684–690, 707–713, 726–732	9,600	0.3	246,800	6.1	256,400	3.7
Point Vicente	679, 701, 702, 718–721, 737–742	1,138,985	39.7	296,347	7.3	1,435,332	20.7
Oceanside	756–758, 801–804, 821–825	--	0.0	470	T	470	T
Santa Catalina Island	759–762, 805–808	193,400	6.8	893,696	22.0	1,087,096	15.7
Santa Barbara Island	743–745, 763–765, 809–811	--	0.0	2,900	T	2,900	T
San Nicolas Island	746–749, 766–769, 812–815, 833–836	--	0.0	264,050	6.5	264,050	3.8
San Diego	842–846, 860–864, 877–882	--	0.0	50,707	1.3	50,707	0.7
San Clemente Island	826–832, 847–852, 865–869	6,550	0.2	60,450	1.5	67,000	1.0
Tanner & Cortes Banks	853–855, 870–873, 888–891, 897	110,000	3.8	32,200	0.8	142,200	2.0
Totals		**1,592,954**	**55.5**	**3,489,653**	**85.9**	**5,082,607**	**73.3**
Pounds of unknown origin not included above		1,276,215	44.5	574,515	14.1	1,850,730	26.7
Total catch		**2,869,169**	**100.0**	**4,064,168**	**100.0**	**6,933,337**	**100.0**

* Interseason—North of Pt. Arguello March 2–July 31
—South of Pt. Arguello March 2–August 31
† Season —North of Pt. Arguello August 1–March 1
—South of Pt. Arguello September 1–March 1

eral fishing area expressed as a percentage of the total for that time period. These general areas are the same groupings used in past yield-per-area reports (Pinkas, 1951) and provide a standard for comparing area of catch.

Catch localities for the 1963–64 season were similar to the 1962–63 season. In 1963–64, 16 percent of the seasonal catch was taken in Monterey Bay (Table 11) and only 2 percent in 1962–63. Santa Catalina Island contributed 22 percent of the total catch in the 1963–64 season. Compared to past years, this represents a significant change in the relative contribution of the Santa Catalina Island area to the total catch. This change resulted from the opening of the southeastern portion of the island, blocks 806 and 807, to roundhaul and purse-seine nets on September 23, 1963. Seiners concentrated on this area shortly after the opening and approximately 200 tons of sardines were taken.

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A NEW SHALLOW-WATER OPHIDIOID FISH FROM THE TROPICAL WEST ATLANTIC

BY

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ABSTRACT. — A new genus and species, *Calamopteryx goslinei,* of viviparous reef-dwelling ophidioid with elongated pectoral radials is described and figured; within the recently expanded family Ophidiidae, it belongs with the genera previously treated as the separate family Brotulidae.

Specimens of this species first came to our attention in collections made on the Academy's fish survey of the inshore waters of the Bahama Islands, a project begun and sponsored by Mr. and Mrs. Charles C. G. Chaplin of Haverford, Pennsylvania. More recent shore collections elsewhere in the tropical West Atlantic that have yielded additional material are: The Breden-Archbold-Smithsonian Biological Survey of Dominica — principal collector, Victor G. Springer; the 1964 Grand Cayman Expedition of the University of Florida and the Academy — principal collectors, Carter R. Gilbert and James C. Tyler; the 1965 Koven Expedition of the Academy — principal collectors, James C. Tyler and William N. Eschmeyer; and collections at Puerto Rico by John E. Randall.

For the opportunity of examining specimens in their care, we thank Ernest A. Lachner and Victor G. Springer (USNM — United States National Museum), and Carter R. Gilbert (UF — University of Florida, Gainesville).

Calamopteryx new genus

Type species. — *Calamopteryx goslinei* new species.

Diagnosis. — Chin barbels absent. Gill membranes barely joined far anteriorly, free from isthmus. Livebearing; genitalia of male consisting of a minute penis enclosed in a fleshy papilla, no claspers or ossified intromittent organ. Ventral fins immediately adjacent to each other, each with a single ray, originating well behind the symphysis of the cleithra, a distance greater than two-thirds the snout length; the pelvic girdle does not extend anteriorly to the symphysis of the cleithra (Fig. 1). Vertical fins confluent, covered with thin skin through which the fin rays are easily visible. Pectoral fin entire, without separate elongated rays, supported by a peduncle which contains the elongated pectoral radials (Fig. 2). Caudal-fin rays ten. Head partly naked, bearing prominent dermal papillae; anterior nostril tubular, located directly above upper lip; developed gill rakers two; tongue with an anterior, prow-like extension. Spine on opercle flattened and flap-like. Branchiostegal rays seven. Body relatively short and stubby, snout depressed. Lateral line interrupted, the anterior portion above the midline of the body, the posterior portion along the midline. Teeth present on premaxillary, vomer, palatine, and dentary; maxillary vertically expanded posteriorly, a small ventrally directed process near the posteroventral angle. Eyes developed, at surface of head. Body completely covered with small, imbricate scales. Peritoneum pale.

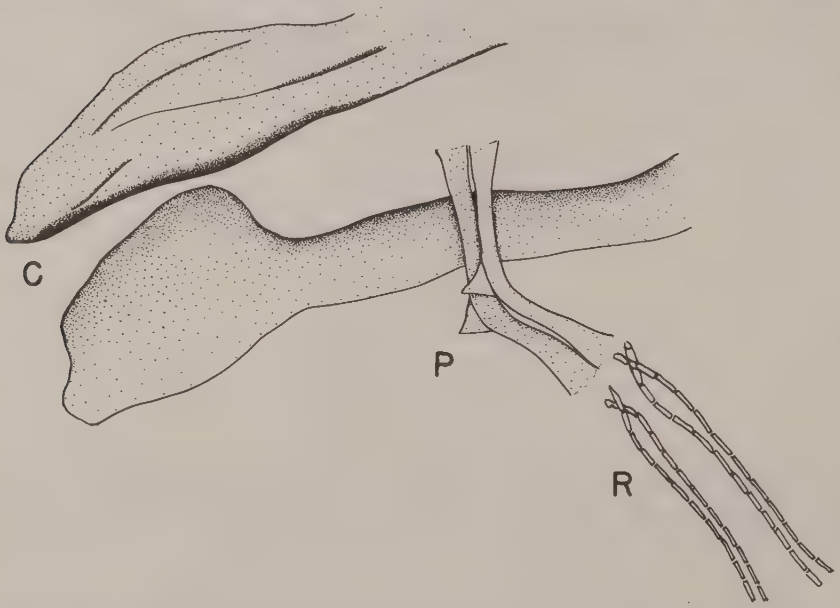

Fig. 1. — *Calamopteryx goslinei.* Alizarin preparation of pelvic girdle showing anterior ends of cleithra (C), pelvic bones (P), and ventral-fin rays (R). Ventrolateral view, anterior to the left. Drawn by Mildred H. Carrington.

First neural spine short; neural spines four to eight depressed; neural spines of abdominal vertebrae not truncate at their tips. Ribs on first centrum modified (? for swimbladder support) in both sexes, ribs on second centrum normal but longer than those following; ribs on vertebrae one to six inserted on centra, those following on parapophyses; epipleurals associated with vertebrae two to 11. Total vertebrae 43 or 44.

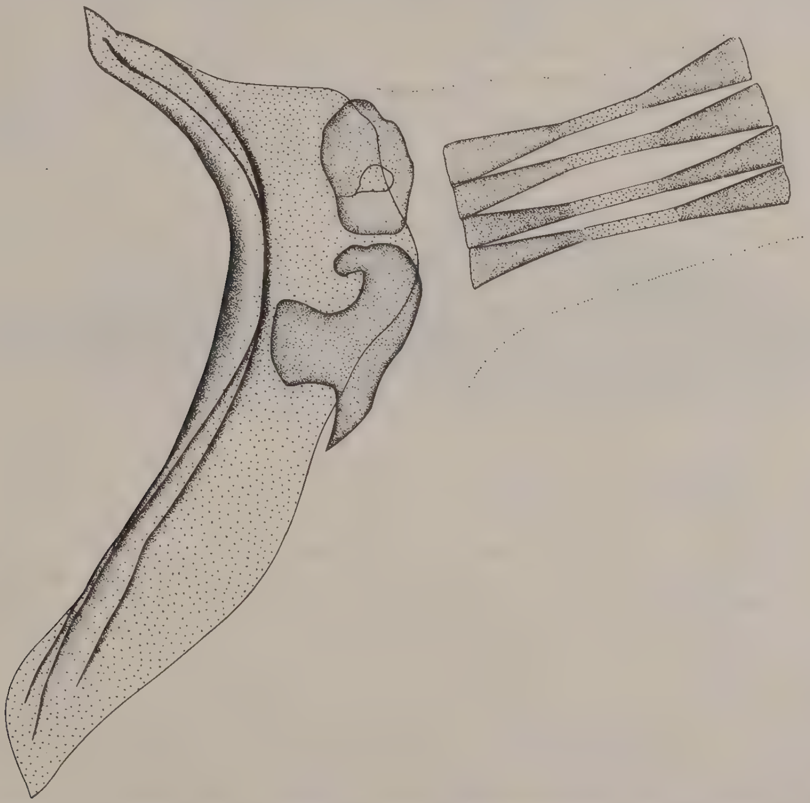

FIG. 2. — *Calamopteryx goslinei.* Alizarin preparation of pectoral girdle. Note elongated pectoral radials. Drawn by Mildred H. Carrington.

Relationships. — Among the viviparous ophidioid genera, *Calamopteryx* is most closely related to those forms in which the male has an intromittent organ with no ossified parts or hard paired claspers (that is to say, not the *Dinematichthys-Ogilbia* group, the Dermatopsini, or *Dipulus,* see Cohen, 1966). This is a large group containing more than a dozen diverse and distinctive genera. *Calamopteryx* differs from all of them in various combinations of characters and does not seem particularly close to any. *Bidenichthys* is perhaps worthy of comparison because it shares with *Calamopteryx* elongated pectoral radials. *Bidenichthys,* however, has a free caudal fin, truncate neural spines on the abdominal centra, and a scaleless head. *Microbrotula* has many characters in common with *Calamopteryx;* however, it differs in having normal pectoral radials, a rounded, needle-like spine on the opercle, the first rib borne on the second centrum, and most important of all a complex and strikingly different intromittent organ which has two fleshy claspers, a median papilla, and a median cartilaginous structure.

The closest relative of *Calamopteryx* remains to be discovered.

Calamopteryx goslinei new species Figs. 1 to 3.

Description. — Figure 3 shows the general appearance of the fish. Measurements of five specimens are given in Table 1 and selected counts in Table 2.

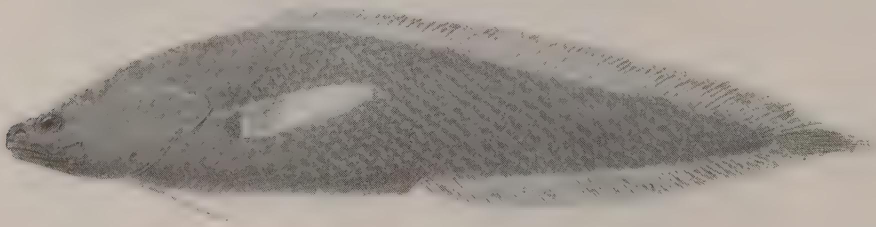

FIG. 3. — *Calamopteryx goslinei.* Holotype, 44.0 mm standard length, ANSP 100892. Drawn by Steven P. Gigliotti.

Head long, its depth at occiput nearly equal to its breadth at that point, the dorsal profile depressed above the eyes. Snout rather broadly rounded. Mouth nearly terminal, the snout projecting but little before it. Eyes large and prominent, with a transparent covering, directed anterodorsally. Anterior nostril tubular, near tip of snout, directed anteroventrally. Posterior nostril a simple hole with raised margins, slightly closer to eye than to anterior nostril, its opening directed posterodorsolaterally. Least width of pigmented interorbital about equal to eye, the area flat, or slightly arched or depressed. Jaws little sloping, long, the maxillary extending back well beyond posterior margin of eye, becoming increasingly broad posteriorly and with a truncate rear margin; a bony knob forms the lower posterior angle of the maxillary. The dorsal rim of the maxillary is sheathed by the suborbital when the mouth is closed. Ventral margin of suborbital sagging notably and deepest below posterior third of the eye, incised upward at the upper posterior end of the maxillary. Skin of snout and chin highly convoluted, with prominent flaps and grooves; the elongate pores along the upper lip line separated by folds of skin are reminiscent of the cusk-eel, *Otophidium dormitator* (Böhlke and Robins 1959: 40, fig. 1, C).

A narrow, compressed, vertical, median rostral spine is present between the anterior margins of the eyes (most easily seen in an alizarin preparation). A curved anteriorly directed spine is present at the angle of the preopercle. Embedded opercular spine thin and flexible, but with a pointed tip. Large, white sensory papillae mark the route of the cephalic lateral line system, and smaller ones course along the lateral lines on the body. The papillae on the body are difficult to count on most specimens; the few counted (all counts questionable) had about 12 to 14 papillae in the upper, anterior lateral line segment (behind upper end of gill opening) and about 29 to 33 in the lower, median segment.

Gills three and one-half. No pseudobranchia evident. On the first gill arches of five stained individuals, there are two or three rudiments on the upper limb and two rakers followed by five to seven rudiments on the lower limb. The rakers are short structures with somewhat swollen, spiny tips. The rudiments are broad, low, and spiny. The tongue is broad and thick basally, then rather abruptly constricted so that its free tip is both narrow and shallow; the roundly pointed tip extends forward to or just beyond the vomerine tooth patch.

Teeth present on premaxillaries, dentaries, vomer and palatines; the following description of dentition is based on five stained individuals. On each premaxillary is a band of tiny villiform teeth, plus two to four considerably enlarged, fang-like teeth in the innermost series at the anterior tip of the bone; the mesial enlarged tooth is longest. On each dentary is a patch of villiform teeth which is flanked on the inside by a row of enlarged, spaced, pointed canines; these are not quite as large as the canines at the head of the premaxillary. A narrow curved patch of tiny villiform teeth on the vomer, with three or four greatly enlarged canines forming a partial posterior series on each leg of the patch; on the right leg of the vomerine patch in one individual, there is a complete row of seven enlarged posterior teeth. On each palatine, the teeth are in a narrow patch that becomes uniserial posteriorly; the teeth of the innermost row are somewhat more enlarged than the others, and these continue back to form the uniserial portion of the patch.

Scales cycloid, overlapping, covering body, cheeks and opercles, and top of head forward to level of posterior margins of pupils, but absent from snout, maxillaries and chin. Scales on the head, and particularly on the opercles, largest. Belly, including the preventral region, completely and evenly scaled. All scales are exposed, easily visible, and regularly arranged, but they are deciduous and many to nearly all are missing from most specimens; between 60 and 70 scales in a longitudinal series were counted (all counts questionable) on five individuals.

The dorsal and anal fins are fully continuous with the pointed caudal fin, which has exserted rays. Origin of dorsal fin from about one-half to an entire pectoral-peduncle length behind a vertical with the bases of the pectoral-fin rays. Pectoral fins long and narrow, their distinctive basal peduncles completely covered with scales. Ventral fins inserted anterior to a vertical from dorsal end of gill opening, but well behind symphysis of cleithra.

Color in alcohol. — Well-scaled small and medium-sized specimens are nearly uniform brown, the dorsal portions before the occiput perhaps slightly darker than the postoccipital regions. The only characteristic markings are a short dark streak extending backward from the eye, a dark streak bordering the upper margin of the maxillary, and the portion of the maxillary itself that is exposed when the mouth is closed. The vertical fins are pale, or they are dusky basally (particularly posteriorly) and pale distally. On many specimens the course of the lateral segment of the cephalic lateral line system is darker than surrounding regions. On one large individual there is more dark pigment on the head than is shown on most others; the course of the lateral canal is dark, as is all of the top of the head anterior to the occiput, the side of the head anterior to the posterior margin of the maxillary, and the entire undersurface of the head including the branchiostegal membranes.

A juvenile individual from the Bahamas (sta. 510, 24.2 mm) shows a distinctive color pattern. A broad brown stripe that runs the length of the fish is median on the posterior two-thirds of the tail but courses upward anterior of that point and is on the upper half of the fish in the trunk region and posterior part of the head. Nowhere does the stripe extend to either the dorsal or ventral profile. This fish is larger than others from the Bahamas and Grand Cayman Island, all of which are pigmented like adults.

Color in life. — A note by John E. Randall with the specimen from Puerto Rico states that it was violet gray, the median fins yellow posteriorly.

Remarks. — The largest known individual of *goslinei* measures 55.7 mm standard length. The species is known from the Bahamas south to the Lesser Antilles, and has been collected at depths ranging from 30 to 180 feet. It apparently is a coral inhabitant, having been taken from small patch reefs and from larger reef structures. Often it has been collected near the point of drop-off to deep water at the edges of banks, where coral growths are low. At the 180-foot station in Puerto Rico, the bottom was hard and there were only a few ledges and a little sand. No individual was seen unless poisoned.

The species is named for our friend and colleague, Dr. William A. Gosline, in recognition of his contributions to knowledge of ophidioid fishes.

Material examined. — HOLOTYPE: ANSP 100892 (44.0 mm standard length, illustrated), sta. 510, Indian Cay, off West End, Grand Bahama Island, Little Bahama Bank; 75 feet; 16 July 1959; R. E. Schroeder, S. Gross.

PARATYPES: BAHAMAS: ANSP 106700 (1, 24.2), taken with the holotype. ANSP 106701 (1, 12.7), sta. 513, N of Green Cay (N of Rose Island), Nassau vicinity, Great Bahama Bank; 50 ft.; 14 Nov. 1959; C. C. G. Chaplin, C. R. Robins, J. E. Böhlke, B. Parker. ANSP 106694 (2, 29.2-43.9), sta. 520, N of the second cay SW of Elbow Cay, Cay Sal Bank; 84 ft.; 1 May 1960; D. K. Farquhar, H. R. Roberts, J. E. Böhlke, H. P. Brown, J. M. Greeven. GRAND CAYMAN ISLAND: ANSP 106695 (1, 22.2) and UF 12340 (1, 29.4), sta. 5, Paradise Rocks, off N end of Georgetown, W side of island; 45 to 50 ft.; 22 Oct. 1964; C. R. Gilbert, J. C. Tyler. ANSP 106696 (1, 24.0), sta. 14, at dropoff, off N end of Georgetown; 100 to 115 ft.; 26 Oct. 1964; C. R. Gilbert, J. C. Tyler. ANSP 106697 (1, 17.4), sta. 16, off S end of Georgetown; 30 to 35 ft.; 26 Oct. 1964; C. R. Gilbert, J. C. Tyler. UF 12341 (2, 18.4-32.4), sta. 21, Paradise Rocks; 65 to 70 ft.; 29 Oct. 1964; C. R. Gilbert, J. C. Tyler. PUERTO RICO: ANSP 106702 (1, 43.6), 6 mi. S of La Parguera; 180 ft.; J. E. Randall. DOMINICA: ANSP 106698 (1, 33.2), sta. TE-44, Prince Rupert Bay, Portsmouth, S side of Prince Rupert Bluff; 85 to 100 ft.; 9 July 1965; J. C. Tyler, W. N. Eschmeyer. USNM 198218 (25, 26.4-55.7, plus 2 cleared and stained) and ANSP 106699 (5, cleared and stained), sta. VGS64-29, Soufriere Bay at Scotts Head; 30 to 45 ft.; 15 Nov. 1964; V. G. Springer, R. H. Reckeweg, R. B. Blatcher.

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TABLE 1. — *Calamopteryx goslinei:* The standard lengths in millimeters, followed by measurements as percentage of standard length of the holotype and four paratypes.

	UF 12341	ANSP 106698	ANSP 106694	ANSP 100892[1]	USNM 198218
Standard length (mm)	32.4	33.2	43.9	44.0	55.7
Total length	113	116	111	113	—
Greatest depth	20	24	22	23	21
Predorsal length	40	39	38	37	38
Preventral length	23	22	22	24	24
Preanal length	52	53	55	53	54
Head length	29	30	28	28	28
Greatest head width	15	16	15	17	16
Head depth at occiput	15	16	16	15	17
Eye diameter	4.9	4.5	4.6	4.1	4.0
Snout length	6.5	6.9	5.9	5.9	5.6
Pigmented interorbital width	5.3	4.8	4.6	4.3	5.2
Upper-jaw length	15	15	13	13	14
Ventral-fin length	14	16	13	—	15
Total pectoral length	25	27	24	24	27
Length middle pectoral ray	21	23	20	20	22
Least width pectoral peduncle	4.3	4.2	3.9	3.9	4.1
Body width at anus	9.0	7.8	8.7	8.0	10
Ventral-fin base to cleithral symphysis	4.0	4.2	4.3	4.8	4.0

[1] Holotype; illustrated.

TABLE 2. — *Calamopteryx goslinei:* fin-ray and vertebral counts of selected type specimens.

Dorsal-fin rays				
66	67	68	69	70
2	2	6	3	2

Pectoral-fin rays		
13	14	15
4	19	6

Anal-fin rays					
52	53	54	55	56	57
6	6	2	—	—	1

Total vertebrae	
43	44
2	3

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THE SUBFAMILY TELLININAE IN THE WESTERN ATLANTIC
THE GENUS TELLINA (Part I)[1]

BY

Kenneth J. Boss[2]

The primary purpose of this monographic study is to review the systematics of the genus *Tellina* and related genera in the Western Atlantic and to present a synthesis of the taxonomy of the group consonant with modern evolutionary theory. The first, and most important step in the realization of this purpose is the recognition and definition of each species. The criteria utilized in the determination of each taxonomic element have out of necessity been morphological. It is purposeful and valuable to study the relationships among the species and within the species-groups, a process which leads ultimately to an arrangement of superspecific categories, which, in their association, reflect the patterns of phylogeny. Along with the presentation of the results of the systematic investigation are the formulation and discernment of generalities concerning the patterns of geographical distribution.

Acknowledgments

Without advice and aid from many persons and institutions, a work of this kind could never materialize, and therefore, to the following people, I would like to acknowledge my appreciation for their considerate help and cooperation. Dr. W. J. Clench, under whose direction most of this work was done, has read the manuscript and given freely of his time for constructive criticism. Dr. R. D. Turner and Miss V. C. Kenk have assisted in reading the text and in preparing some of the plates. Members and associates of the Department of Mollusks at Harvard University have served in various capacities and deserve many thanks; these include: Messrs. A. Merrill, R. W. Foster, R. I. Johnson and Miss M. L. Smith. Miss C. Martin, Mrs. B. Crowley and Mrs. M. Carrington have helped with the inking and preparation of the illustrations. Institutions and many private individuals have been helpful in the exchange and loan of specimens; these include: The Trustees of the British Museum (Natural History) and members of its staff, Messrs.

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[1] The subfamily Tellininae will appear in 3 parts, as Johnsonia, number 45 [*Tellina* (Part I)]; number 46 [*Tellina* (Part II) and *Tellidora*], and number 47 [*Strigilla*]. The plates are numbered consecutively and some of those referred to in this number will be published in number 46.

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N. Tebble, P. Dance and C. P. Nuttall; Drs. H. Rehder and J. Rosewater of the United States National Museum; Drs. R. T. Abbott and R. Robertson of the Academy of Natural Sciences of Philadelphia; Mrs. G. Warmke of the Institute of Marine Biology of Puerto Rico; Dr. A. Clarke of the Canadian National Museum; Mr. P. Morris of the Peabody Museum of Yale University; Dr. E. Binder of the Muséum d'Histoire Naturelle in Geneva; Dr. J. Knudsen of the Universitetets Zoologiske Museum in København; Dr. C. O. van Regteren Altena of the Rijksmuseum van Natuurlijke Historie, Leiden, Netherlands; and, Messrs. A. A. Olsson, D. Schmidt, R. Parker, and R. Bullock. Financial aid from the Society of Sigma Xi and the Department of Biology, Harvard University, enabled the author to complete this study.

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ABBREVIATIONS

ANSP	Academy of Natural Sciences of Philadelphia
BMNH	British Museum (Natural History)
CM	Charleston Museum
CNM	Canadian National Museum
IMBPR	Institute of Marine Biology of Puerto Rico
MCZ	Museum of Comparative Zoology, Harvard University
USNM	United States National Museum
ZMK	Universitetets Zoologiske Museum, Kõbenhavn

Historical Note

The nominate genus *Tellina* dates from Linnaeus, but it was well established in the pre-Linnean literature. According to Jeffreys (1863), the generalized name, 'tellen', was introduced by Dioscorides of Anazarba in the first century. No doubt, the term had an even greater classical antiquity, since *Tellina* and its near relatives in the Tellinacea were held in high regard for economic reasons, particularly as food. In the Linnean definition of the genus, twenty-five species were included, of which nineteen remain in the confines of the Tellinidae as it is presently understood; the remaining species have been assigned to other groups. Hanley (1855) and Dodge (1952) have discussed the Linnean species and their relation to the Linnean conchological collection.

By the end of the 18th century, a number of additional species of *Tellina* had been described and Spengler (1798) had published the first treatise to deal solely with the genus. His work is valuable in that locality data are given for each species and that, by citation, the nonbinomial but important work of Chemnitz becomes available.

The first important monograph of the genus in the 19th century came with the work of Hanley (1846). In the Thesaurus Conchyliorum, Hanley delineated the known species of *Tellina* with little regard for subgeneric organization. The same may be said for the Conchologica Iconica of Reeve in which Sowerby (1869) treated the genus *Tellina*.

Römer (1870–73) produced a more exhaustive treatise on the Tellinidae and employed a conservative approach to the breakdown of the family into genera and subgenera. Later, Bertin (1878) discussed the family in general terms of zoogeography, elevated a number of subgeneric categories to the generic level, and delineated the known species preserved in the Museum d'Histoire Naturelle, Paris. The fruition of these various labors culminated in the works of Dall (1900a, b). His work still ranks as the most serious attempt to arrange the infrageneric groups in a meaningful scheme. More recently Afshar (1950), in an unpublished study of recent and fossil forms, has revised the generic and infrageneric taxa of the family.

Tryon (1869) and Paetel (1890) have catalogued the specific names in the family and Salisbury (1934) has delineated most of the superspecific categorical names. The best sources for type designations of superspecific groups include Schmidt (1818), Children (1823), Gray (1847), Kobelt (1878), Stoliczka (1870), and Dall (1900b).

Broad and general works dealing with the arrangement of subgenera and the placement of species include H. & A. Adams (1856), Fischer (1887), and Thiele (1935).

The early work of Say and Conrad provides a basis for the knowledge of the eastern American continental fauna and the descriptive treatises of d'Orbigny constitute the fundamental assessment of the Antillean and South American faunas. Dall (1900a) gave a synopsis of the North American species, and Dall and Simpson (1901) treated the Puerto Rican forms. Recently, Warmke and Abbott (1961) have reviewed in general terms the species of the Caribbean. Numerous smaller but no less significant works have dealt with more restricted geographical areas.

The fossil history of the Tellininae in the Western Atlantic has been largely revealed through the work of Dall (1900b), Woodring (1925), Maury (1917; 1920) and Gardner (1928). In the general discussion for each taxon in the present work, pertinent remarks are made concerning the fossil record.

The basis of the faunal comparison between the tellini-form species of the Western Atlantic with that of the Eastern Pacific rests on the rather extensive literature on the bivalves of the Panamic Province. Dall (1900a) described a number of species from the Eastern Pacific and listed the occurrence and range of each. Hertlein and Strong (1949) and Keen (1958) have contributed greatly to the knowledge of the Eastern Pacific fauna, and Olsson (1961) has summarized the work of the early writers and presented a well illustrated and monographic treatment of the bivalves of that area.

SHELL MORPHOLOGY

The morphological characters of the shell are of great importance in the systematics of the Tellinidae (Plate 127). In a great measure, some of the most distinctive anatomical features are reflected in conchological characteristics so that great reliance upon 'hard-part' morphology is justified. In general, the higher categories in bivalve mollusks are determined to some extent upon the structural nature of the hinge and ligamental mechanisms; however, the number and placement of muscle scars and the structural nature of the ctenidia are also very important. At the generic and subgeneric levels in the Tellinidae, the most important traits include: 1, the structure, placement, and strength of the dentition of the hinge; 2, the configuration of the pallial sinus and its relationship to the pallial line and the adductor muscles; 3, the placement, extent, and development of the ligament; and 4, the peculiarities of external sculptural differentiation. In addition, the shape and size of the shell as well as its external and internal coloration have some measures of validity in the delineation of taxa.

The hinge of the Tellinidae always possesses two cardinal teeth, which are referred to as constituting the cardinal complex. These structures which rest upon a variously thickened lateral or cardinal plate are situated beneath the umbo and serve to interlock the valves. At least one of the two cardinal teeth in each valve is bifurcate and is herein referred to as the bifid cardinal tooth; the other is generally a single structure and is herein called the laminate cardinal tooth. In the left valve, the bifid cardinal tooth is always in the anterior position while the laminate cardinal is posterior. The configuration of the cardinal complex in the right valve is reversed; the bifid cardinal is posterior and the laminate cardinal is anterior. The cardinal teeth exhibit but a small range of variation from species to species and are therefore of little use for specific identification. However, the lobes of the bifid cardinal are of variable size and they may be skewed from the dorso-ventral axis of the shell, in which case they assume some taxonomic importance. Likewise, the thickness and length of the laminate cardinal may function in the discrimination of species.

The presence of lateral teeth distinguishes the Tellininae from the Macominae, which are laterally edentate. The lateral teeth in the Tellininae are differentiated projections

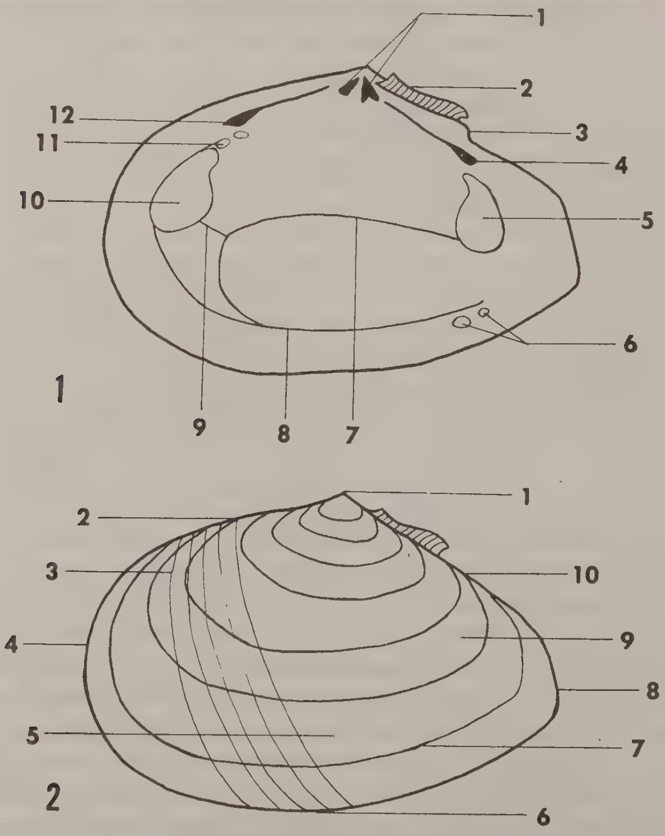

Plate 127. Diagrammatic representation of the shell morphology of a generalized *Tellina*. Fig. 1. Internal view of a right valve. 1. Cardinal complex with the single anterior laminate cardinal tooth and the bifid cardinal tooth. 2. Ligament. 3. Nymphal callosity. 4. Posterior lateral tooth. 5. Posterior adductor muscle scar. 6. Cruciform muscle scars. 7. Pallial sinus. 8. Pallial line. 9. Interlinear scar. 10. Anterior adductor scar. 11. Pedal retractor scars. 12. Anterior lateral tooth. Fig. 2. External view of a left valve. 1. Umbo. 2. Anterior dorsal margin. 3. Oblique sulcus or scissulation. 4. Anterior margin. 5. Disc. 6. Ventral margin. 7. Concentric sculpture. 8. Posterior margin. 9. Posterior slope. 10. Posterior dorsal margin.

of the hinge line and interlock as well as stabilize the position of the two opposite valves. The maximum number of laterals is four, that is, two in each valve. The one behind the cardinal complex in the vicinity of the end of the ligament is called the posterior lateral, the other in front of the cardinal complex is the anterior lateral. In the left valve, the lateral dentition is less strongly developed than in the right valve. In most groups the right valve possesses the greatest development of the lateral teeth and, in particular, it is the right anterior lateral tooth which maintains the greatest strength while often the posterior lateral is diminished. Sockets or fossae for the interlocking of the teeth in opposite valves are sometimes developed. The position of the right anterior lateral tooth assumes some importance as a taxonomic character because it is variously placed in relation to the cardinal complex. In groups like *Eurytellina* and *Angulus*, this tooth is proximal to the cardinal complex whereas in *Tellina* s.s. and in *Tellinella*, the tooth is distal to the cardinal complex.

The ligament is opisthodetic or posterior to the umbos and mostly external. It consists of a horny external sheath which is yellow, brown, or black in color and of an internal, fibrous, calcareous element which is white. The nymph subtends the calcareous element of the ligament and consists of a thickened portion of the dorsum of the shell. When the nymphs are greatly thickened and protuberant, they are termed nymphal callosities. Trueman (1949) has discussed the structure of the ligament in *Tellina tenuis* in great detail.

The form of the ligament varies from the extremely long and narrow, as in *Phylloda*, to the short and high, as exemplified by *Angulus*. The nymphal callosities tend to be better developed in thin shells with a short ligament, and in the main, suborbicular species have a short ligament. In *Tellidora*, there is a tendency for the ligament with its calcareous element to become internal, as in the related family Semelidae.

The internal surface of each valve bears a number of muscle scars which delimit the attachment of muscles to the shell. Plate 127 illustrates these muscle impressions and their associated structures. The anterior adductor muscle tends to be long and narrow while the posterior adductor is more or less rounded to subquadrate. Dorsal to the adductors are the scars of the pedal musculature; the anterior pedal retractor impresses the greatest complex of scars along the anterior dorsal border of the shell and may, in fact, be largely confluent with the anterior adductor muscle. From the base of the posterior adductor the pallial sinus takes its origin. The siphonal musculature forms the scar of the definitive pallial sinus which extends anteriorly and which may or may not be confluent with the anterior adductor muscle. Ventrally the pallial sinus usually unites with the pallial line. If the pallial sinus does not touch or become confluent with the anterior adductor muscle scar, the distance which separates them may be traversed by a linear scar. In many cases the linear scar is absent and no direct connection exists between the sinus and the anterior adductor. Far posteriorly and closely aligned to the terminus of the pallial line are the cruciform muscle scars. These are four in number, two for each valve. In general, the scars are rounded, but the anterior one in the right valve tends to be rectangular.

The microscopic structure of the shell has been described by Trueman (1942). The periostracum is made up of a horny substance. The calcareous portion of the shell is aragonitic and divided into three layers of different crystallographic properties.

The external sculpture is predominantly concentric. Sulci of varying strength generally separate the broad concentric bands or narrower raised lirations. Dorsally the concentric sculpture may become differentiated into spinosities, particularly along the posterior slope. Radial sculpture is rare and in no case does it occur alone; therefore, a number of species present a pattern of cancellate sculpture. Acentric sculpture consisting of oblique sulci which cross the rectangular concentric sculpture is typical of a number of tellinid groups, particularly *Scissula* and *Strigilla*. This pattern of sculpture is herein referred to as being scissulate, and the oblique sulci are termed scissulations.

The sculptural pattern and thickness of the valves are adaptive characteristics which may be correlated with environment. Heavily shelled species, such as the European *Tellina crassa*, are found in substrates of coarse sand and shelly gravel whereas the thinly shelled species, such as *Tellina agilis*, occur in muddy sands. The sculptural pattern may be responsible for the maintenance of position in the substrate. Some *Tellina* live vertically whereas *Macoma*, which rarely tends to be sculptured, lies on its side in a horizontal position. Unfortunately, a quantitative evaluation of the adaptive significance of these characteristics is lacking.

ANATOMY

The following discussion is based largely on dissections of *Tellina alternata* Say and *Tellina punicea* Gmelin, both representatives of *Eurytellina*. These dissections were, except from minor portions, executed by Miss Vida C. Kenk of the Department of Mollusks, Museum of Comparative Zoology, Harvard University. Many of the statements concerning specific morphological traits have been derived from the literature. The European species, particularly the British species, of *Tellina* are best known from the morphological works of Atkins, Graham, and Yonge. Pelseneer laid the foundation for some comparative work on the species of the East Indies in his general discussion of pelecypod morphology in the Siboga report (1911). The anatomical features which are discussed below are illustrated on Plate 128.

Mantle. The mantle is thin and transparent. It is united dorsally and fused posteroventrally in the region of the cruciform muscle where it is thickened at its edge. The pedal gape is large and extends ventrally from the anterior adductor muscle to the cruciform muscle. Posteriorly the mantle is modified to form portions of the siphonal apparatus and musculature.

Foot. The foot is large, generally laterally compressed and quite active. Yonge (1949) has described its great mobility and usefulness in burrowing. Pelseneer (1911) has shown that some species develop a plantar surface on the foot. The vestigial pedal gland and remnants of the byssiferous apparatus have been studied in detail by Carriere (1879) and Barrois (1885). A functional byssus is absent in the adult stage.

Musculature. The morphology of the musculature has been reviewed by Graham (1934b) who made a comparative study of the myology of selected members of the Tellinidae and related families. The anterior and posterior adductors are large and well developed. The anterior adductor is subdivided into two or three parts, the largest of which is ventral; the muscle tends to be irregularly elongate and semilunate in shape. The posterior adductor tends, on the other hand, to be more or less quadrate. A medial adductor courses through the viscera in the vicinity of the appendix of the stomach and is attached to both valves anterior to the cardinal complex in the umbonal cavity. The extrinsic pedal musculature consists of anterior and posterior pedal retractors and of a pedal protractor; the entire complex of pedal musculature inserts into the foot. The narrow origin of the protractor pedis is immediately dorsal to the largest portion of the anterior adductor muscle and ventral to the origin of the anterior pedal retractor. The protractor splays out superficially over the foot.

The anterior pedal retractor which is generally separated from the protractor pedis by a small division of the anterior adductor muscle, forms a trigonal attachment along the anterior dorsal margin. The anterior retractor inserts deeply into the foot, lies under the protractor pedis fibers and portions of the posterior retractor although some of its fibers lie over those of the posterior retractor. Another section or portion of the anterior adductor is present along the anterior dorsal margin above the origins of the anterior pedal retractor. There are no elevator pedis muscles.

The posterior pedal retractor makes an oval attachment dorsal to the posterior adductor muscle along the posterior dorsal margin of the valve. This pedal muscle courses anteriorly through parts of the kidney into the foot where its fibers lie beneath the superficial fibers of the pedal protractor and intermesh with the fibers of the anterior pedal retractor.

The foot and viscera possess many intrinsic adductor muscle fibers while special siphonal muscles and the cruciform muscles are developed posteriorly. The pallial muscle defines the size and placement of the pallial sinus or cavity and generally is coextensive with the

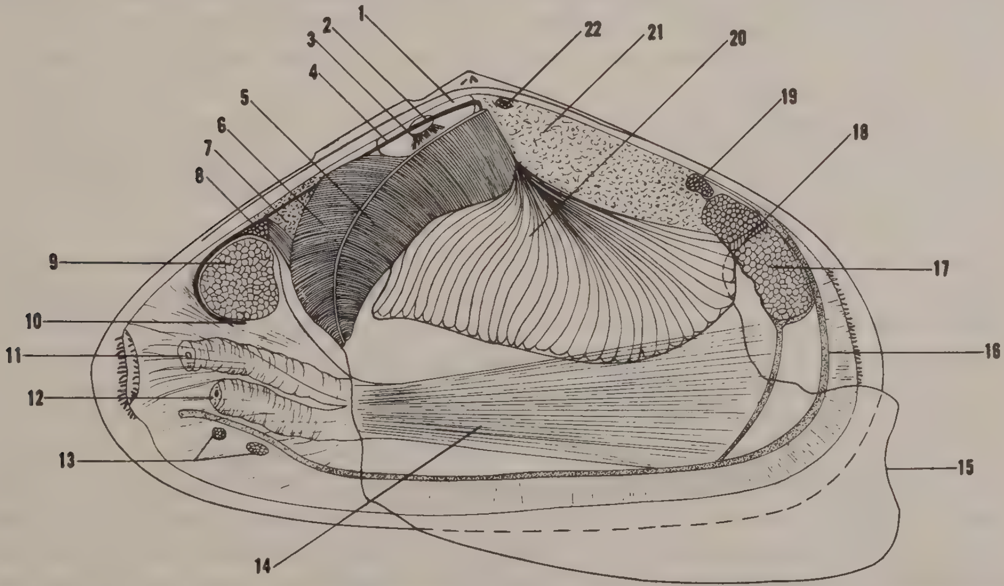

Plate 128. Semidiagrammatic illustration of the anatomy of *Tellina* (*Eurytellina*). Fig. 1. Specimen with the right valve removed to show general structural features. 1. Pericardium. 2. Ventricle. 3. Auricle. 4. Rectum. 5. Inner demibranch. 6. Outer demibranch. 7. Kidney. 8. Posterior retractor muscle. 9. Posterior adductor muscle. 10. Anus. 11. Excurrent siphon. 12. Incurrent siphon. 13. Cruciform muscles. 14. Siphonal retractor muscle. 15. Foot. 16. Pallial muscle. 17. Anterior adductor muscle. 18. Pedal protractor muscle. 19. Posterior retractor muscle. 20. Labial palps. 21. Digestive gland. 22. Medial adductor muscle.

muscular lobes of the mantle ventrally. A short supportive interlinear muscle may connect the anteriormost extension of the pallial muscle with the anterior adductor muscle.

Cruciform muscle. The posterior portion of *Tellina* is highly specialized. The cruciform muscle, a structure found only in the Tellinacea (see Graham, 1934a, b; Yonge, 1949), possesses a sensory pit and associated sensory structures as well as the uniquely crossed muscles. Deshayes (1848) pictured the muscle and its concomitant scars which are impressed on the shell. Von Ihering (1901) proposed that the muscle acted as an additional adductor and Graham (1934a) proposed the notion that the muscle and its associated sensory structures were used for water testing. Hoffman (1914) suggested that this sense organ in *Tagelus* functions in the perception and the regulation of blood-pressures in the neighborhood of the siphons. Yonge (1949) agreed with Graham (1934a) that the contention of von Ihering is hardly feasible but disagreed with Graham in pointing out that *Tellina* live deep in the substrate and that water detection would hardly serve a useful purpose, inasmuch as the siphons bring in water from the substrate, at least twenty centimeters away. It might further be suggested that a chemorecepter is probably present in the structure of the siphonal organ and that an additional organ serving a similar purpose is hardly necessary. Yonge contends that the function of the cruciform muscle and organs is one of proprioception. The muscles themselves acting as a supportive structure for the highly extensile siphons and the sensory pit informing the animal of the relative position of the siphons. He argues that the siphons which are very large must be retracted before the mollusk can move with its foot. Since the movement of these structures is probably not a simultaneous one, the cruciform organ may serve to inform the animal about the conditions of blood pressure. It is of interest to note that the siphons of *Macoma* may be found 'swimming' over the substrate, after having been clipped by the edge of the valves during a quick closure.

According to Graham (1934a), *Tellina* and *Macoma* may be differentiated by the nature of the sensory pit associated with the cruciform muscle. In *Macoma*, the pit is connected to the environment by means of a narrow, short tube whereas in *Tellina* it is directly in contact with the external medium.

Siphonal and parasiphonal organs. Another complex of structures is associated with the incurrent siphon. These include the unilateral siphonal and paired parasiphonal organs. They were shown in *Tellina nitida* by Deshayes (1848), and were depicted in *Tellina planata* by Poli (1795), although he did not specifically mention them. Pelseneer (1911) noted the 'organe sensoriel siphonal' or 'valvule palleale' in *Tellina carnicolor* and *T. pretiosa.* Yonge (1949) discussed them as the mantle folds in the Tellinacea and compared them with similar structures in the Mactracea. The same structures in *Temnoconcha* have been illustrated by Boss and Kenk (1964). It is probable that the paired parasiphonal organs are used to keep pseudofaeces from being swept into the gill by the forceful incoming current, to act as valves covering the aperture of the incurrent siphon, and to direct the incoming particles to the distal portions of the ctenidia. The unique siphonal organ is probably associated with the detection of the quality of inflowing water. Both structures appear to be well innervated and a small ganglion is present in the tissues of the siphonal apparatus.

Ctenidia and palps. The ctenidia and the labial palps are the most conspicuous organs in the mantle cavity. Generally the palps are smaller than the ctenidia in *Tellina* while the reverse situation may obtain in *Macoma*, although there are exceptions. The exact proportional relationship between palp size and ctenidial size may be an environmental corollary associated with substrate. The palps are plicate and generally somewhat trigonal in shape. They may be folded somewhat in the mantle cavity so that particular grooves are developed which lead to the mouth, and they are generally contiguous with the anterior boundary of the inner demibranch along a line which has been called the 'distal oral groove' (Kellogg, 1915; Graham, 1937).

The structure of the gills in the Tellinidae has been summarized by Ridewood (1903). The gill is unique. Its anterior portion lacks the outer demibranch and the inner demibranch alone extends dorsally and superficially over part of the pericardium. Centrally and along most of the ctenidial length, the outer demibranch is present and consists of a single dorsally upturned direct lamella. Posteriorly and distally, the lamella of the outer demibranch infolds to form a downwardly-directed portion. The lamellae of both demibranchs are flat and homorhabdic.

The ciliation of the gills has been discussed and described by Kellogg (1915) for *Macoma secta*, Graham (1937) for *Tellina crassa* and Atkins (1937a, b) for *Tellina donacina*, *T. fabula*, *T. tenuis*, *T. crassa*, and *Macoma balthica*. Yonge (1949) corroborated the findings of Atkins. In most species, food particles are carried across the inner demibranch in an antero-ventral direction in the ventral food groove to the labial palps and thence to the mouth. Specific differences, including the presence of supplementary food groove and alterations in kinds of ciliation are recorded by Atkins (1937b). By means of ciliary currents in the mantle cavity, pseudofaeces are collected ventrally at the siphonal organs and are expelled through the incurrent siphon. As Yonge (1949) noted, the sand grains expelled with the pseudofaeces are the largest taken into the mantle cavity; smaller grains enter into the digestive system.

Alimentary canal. The structure of the alimentary canal was figured by Deshayes (1848) for *Tellina nitida*. The functional and adaptive significance of the morphology of the digestive system has been illuminated by the work of Graham (1949), Yonge (1949), Owen (1955) and Purchon (1960). The relatively long, straight oesophagus enters the stomach anteriorly. The stomach consists of a medial globular portion and a postero-ventral extension, the style sac, which is typically united with the midgut. The style sac contains a large crystalline style which abrades against a well developed gastric shield located dorsally in the globular portion of the stomach. This latter portion of the stomach is invested with a complex of ciliated grooves and ridges which direct particulate matter into or out of the caeca of the stomach. Graham (1949) in his description of *Tellina crassa* identified right and left caeca which are antero-ventral and which are coextensive with the right and left lobes of the digestive gland, via a specific number of ducts. In addition, he described a dorsal pouch which is not connected with the digestive gland. The dorsal caecum is however in some species provided with connections to the left lobe of the digestive diverticula. Yonge (1949) added the postero-dorsal or posterior caecum which Purchon (1960) mercifully proposed to call the appendix, relieving the already congested vocabulary. This latter structure, the appendix, was overlooked by Graham (1949). Beneath the appendix courses the previously mentioned medial adductor muscle. As explained by Yonge (1949), the appendix serves as the receptacle for intermediate sized sand grains which are later triturated by the action of the revolving crystalline style. Sand grains found in the compacted faeces, or faecal pellets, in the ascending portions of the midgut and posteriorly, are of a smaller size. With regard to the size and extent of the appendix, Yonge (1949) found that *Macoma balthica* possessed an unusually large structure filled with sand grains. Such an observation is comparable to conditions in *Macoma secta* as reported by Kellogg (1915), who found large quantities of sand in the intestine of this species.

The right and left caeca are connected by the major typhlosole and its concomitant intestinal groove. According to Yonge (1949), the dorsal caecum is connected via the proximal groove with the right or 'food sorting' caecum. The precise movement of materials into, out of, and between each caecum, as well as along the proximal and intestinal grooves is complex and still not fully explained and described. It is sufficient to say that sorted material of small size enters the respective caeca and from there is taken into the branching tubes and pouches of the digestive diverticula where intracellular digestion occurs. All three of the caeca may possess ducts connecting with the digestive gland. The occurrence of phagocytosis and other phenomena associated with movement of particles and digestion in the digestive diverticula have been discussed by Owen (1955). It must be remembered that extracellular digestion is instigated by the enzymes of the crystalline style and that the digestive diverticula, even though associated with the caeca may also connect directly with the globular portion of the stomach itself.

The midgut, combined with the style sac proximally arises independently in an ascending portion before going through a number of complex convolutions. Distally in the ascending portion, faecal pellets are formed. Yonge (1949) and Moore (1930; 1931) have discussed the size, shape and consolidation of the pellets in relation to the midgut length. In this regard, it is important to note that the complex convolutions of the midgut are greater in such species as *Macoma balthica* than they are in *Tellina tenuis*. This is another possible generic distinction first noted by Graham (1934b) and correlated by Yonge (1949) with the intake of mud.

Purchon (1960) has aptly summed up the structural features of the stomach of the Tellinidae in his comprehensive and analytic discussion of the 'Stomach Type V' in the Eulamellibranchia. In short, the major features include: 1) an oesophagus which enters the stomach anteriorly; 2) a union of the style sac with a portion of the midgut; 3) a crystalline style which projects into the stomach and revolves upon the shield on the entad surface of the dorsum of the stomach; 4) a minor and major typhlosole; 5) a left dorsal anterior pouch or caecum; and, 6) a number of specific sorting areas.

The midgut nominally terminates with the beginning of the rectum at its entrance into the pericardium. The rectum traverses the ventricle, passes out the pericardium, continues around the dorsal and ectad surface of the posterior adductor muscle to terminate in an anus near the opening of the excurrent siphon.

The reno-pericardial structures. The heart in *Tellina* is of a simple form. The pericardium is located dorsally between the kidney and the digestive diverticula and may be superficially covered by the dorsal extension of the inner demibranch. The heart itself consists of two large, laterally paired, thin-walled auricles connecting with a single medial, muscular ventricle which is traversed by the rectum. Dorsal aortae extend anteriorly and posteriorly from the ventricle. Deshayes (1848) has discussed in considerable detail the ramifications of the vascular system in *Tellina nitida*. White (1942) has reported the presence of glandular matter in the mantle of *Tellina crassa* which was taken to be the remnants of the pericardial gland. The pericardial organs do not appear to be very well developed in *Tellina*. The pericardium is coextensive with the kidney by means of the paired ciliated funnels.

Odhner (1912) has discussed the reno-pericardial structures in the Tellinidae: his descriptions are based on the anatomy and histology of *Tellina* [*Macoma*] *balthica* and *Scrobicularia nitida* [which is presently referable to the Semelidae]. The gross anatomy of the macomoid *Temnoconcha* has been discussed by Boss and Kenk (1964). In *Tellina alternata* and *T. punicea*, the kidney and its associated structures are essentially alike and do not depart from the general structural features as described by Odhner.

The kidney lies between the heart and the posterior adductor muscle and is traversed by portions of the posterior pedal retractor. As in *Gari tellinella* (Graham, 1934b), the right and left kidneys are united medially, putting them into broad communication. Paired ciliated funnels connect the cavity of the pericardium with the central and proximal portions of the kidney. The nephroproct empties into the urogenital sinus, a common cavity into which the gametes are also released.

Nervous system. The structure of the nervous system conforms to the usual pattern of the lamellibranchs and is quite similar in its general aspects to that of *Psammobia vespertinalis* (Duvernoy, 1853) and *Gari tellinella* (Graham, 1934b). Paired cerebropleural ganglia are located anterior to the fusion of the labial palps on the entad surface of the anterior adductor muscle. These ganglia, which are united by a thin dorsal commissure, give rise to the anterior pallial nerves which course over the external surface of the anterior adductor muscle and innervate the pallial muscles of the mantle and to a short ramus which enters the anterior adductor muscle directly. Individual medially directed rami enter the labial palps. Extending postero-ventrally from the cerebropleural ganglia are the cerebropleural pedal connectives which lead to the closely juxtaposed pedal ganglia in the foot. The presence of otoliths has been indicated for an unidentified *Tellina* by von Ihering (1876) and for *Tellina assimilis* and *T. fabula* by Pelseneer (1911). The pedal ganglia also send out branches which innervate the intrinsic muscles of the foot, certain portions of the alimentary canal, the digestive diverticula and the pedal retractors. Extending posteriorly from the cerebropleural ganglia are the cerebropleural-visceral connectives which communicate with the developed, large and partially united visceral ganglia. Running antero-dorsally from the visceral ganglia are the branchial nerves which ramify in the ctenidia. A small anterior nerve enters the kidney. A distinct ramus innervates the posterior adductor muscle and forms the dorsal pallial nerve. A large ventral ramus descends from the visceral ganglion to divide into a number of subsidiary rami which serve the various organs associated with the siphonal apparatus. The development of the nerves of the ventral ramus is complex. There is a divided ramus for the siphonal retractor muscles, another branch which divides sending a ramus into the cruciform muscles and another into the siphonal organs. Still another major nerve divides to enter the incurrent and excurrent siphons.

Reproduction. Tellina is dioecious. The gonad is imbedded in the foot and surrounds much of the style sac and midgut, extending dorsally and posteriorly in the viscera to the pericardium. The oviduct or vas deferens debouches reproductive products in the common urogenital sinus (Odhner, 1912).

The time of spawning appears to vary by species and geographical locality. Sullivan (1948) found that larval *Tellina agilis* were available at Prince Edward Island, Canada, from July to August while Odhner (1914) found that certain Adriatic *Tellina* have a fifteen day pelagic stage in mid-May. Lovén (1848) has pictured the young stages of an unidentified *Tellina* and Rees (1950) noted the taxodont dentition of the provinculum and the early development of the cardinal dentition. The settling spat of *Tellina* appear to be brightly colored, particularly with purple umbonally.

The pelagic larval stage and its length permit the distribution of species by currents. Those species with a greater range probably have longer larval periods whereas those with shorter pelagic stages may tend to have a restricted distribution. The substrate specificity for settling larvae has never been investigated, but the specificity exhibited by the adults can be used as a criterion in the interpretation of barriers to distribution. Impenetrable substrata are totally unsuitable and most species are adapted to the sand or mud habitat. Rocky coasts, coral reefs, or hard-packed sand are unsuitable habitats and may serve as minor features in the isolation of populations. Unfortunately, the state of the present knowledge of the period of larval development in the Tellininae is so poor that statements as to the relationship between range and length of pelagic stage can only be inferential.

Zoogeographical Considerations

Table I summarizes the distributional data for the subfamily Tellininae in the Western Atlantic. Tables II and III present a delineation of the patterns of allopatry in species-groups between the Western Atlantic and the Eastern Pacific and within the Western Atlantic.

Excepting *Acorylus*, all the Western Atlantic superspecific groups are polytypic. Groups of species representing each generic or subgeneric category are represented in the fauna of the Eastern Pacific or the Indo-Pacific. In general, it may be said that those groups poorly represented in the Western Atlantic are well developed in the Eastern Pacific and, vice versa. Thus, *Tellinella*, represented by *T. listeri* in the Western Atlantic and *T. cumingii* and *T. zacae* in the Eastern Pacific, has numerous representatives in the Indo-Pacific. Similarly, *Angulus* and *Eurytellina*, as herein defined, are very richly developed in the Western Atlantic and Eastern Pacific, but not as highly differentiated in the Indo-Pacific. Western Atlantic species are clearly more closely allied to those of the Indo-Pacific than to either the Eastern Atlantic or the Mediterranean; however, a number of groups well represented in the Indo-Pacific are not present in the Western Atlantic.

When a comparison of superspecific categories is made for the Western Atlantic and the Eastern Pacific, only three of the Western Atlantic groups are absent from the Eastern Pacific. *Tellina* s.s., *Arcopagia*, and *Acorylus*, mostly large and conspicuous elements of the Western Atlantic fauna, do not occur in the Eastern Pacific. The large and polytypic subgenera, *Eurytellina* and *Scissula* are nevertheless less well developed in the Western Atlantic, whereas *Angulus* appears to be more or less equally well developed in both areas.

Numerous authors have proposed faunal provinces for the Western Atlantic Ocean. Ekman (1953) discussed the problem in general zoogeographical terms. Much of his information regarding the distribution of mollusks is derived from von Ihering (1907;

1927). In a recent review, Coomans (1962) has summarized the faunal provinces of the Atlantic coast of continental North America with particular reference to the Virginian Subprovince. The following scheme is employed herein. Six provinces and five subprovinces are adopted. The Arctic Province extending from the polar area to Newfoundland has no representative of the subfamily Tellininae and is therefore beyond the scope of the present discussion. The Nova Scotian Province is boreal and extends from Newfoundland to Cape Cod. The Carolinian Province extends from Cape Cod to Eastern Florida in the vicinity of Cape Canaveral (=Cape Kennedy) and thence to the Gulf of Mexico from Cape Sable, Florida, to the vicinity of Veracruz, Mexico. The West Indian or Antillean Province is bounded by Cape Canaveral (=Cape Kennedy) and Key West, Florida, and the Golfo de Campeche near Veracruz in the north and extends south to Brasil. It may be divided into the Caribbean Subprovince which includes some of the Gulf of Mexico and the Caribbean Sea and is bounded on the south by Trinidad and the Gulf of Paria. The Brasilian Subprovince extends south of the Tropic of Capricorn to Santa Catharina. The Argentinian Province extends from southern Brasil to the Golfo de San Jorge, Argentina. South of the Argentinian Province is the Magellanic Province which because of a lack of representatives of the subfamily is omitted from the discussion.

The distributional data presented in Table I shows that only a single species, *T. agilis*, may be considered boreal while the remaining number of species are temperate, subtropical, or tropical. Thus, it is justifiably observed that the subfamily is predominantly Antillean or West Indian, for, excluding *agilis*, only two species, *T. versicolor* and *T. tenella*, normally occur in the Virginian Subprovince as far north as Cape Cod. Cape Hatteras is a geographic feature which demarcates the northernmost range for fourteen species, five of which are probably advectitious to the offshore shallows at Cape Hatteras. These include *T. listeri*, *laevigata*, *fausta*, *squamifera*, and *americana*. The presence of small and immature individuals actually constitute the records for these species in the north and indicate the absence of an adult breeding population. It is most probable that the larvae of these species have been transported from the south by the currents of the Gulf Stream. The same may be said for the records of *T. radiata* and *T. cristallina* in South Carolina. North of Cape Canaveral (=Cape Kennedy) and in the vicinity of Saint Augustine, two species, *T. lineata* and *T. tampaensis* have their northernmost range extension. The area near Lake Worth, Palm Beach, and Miami serves as a point of delimitation of the range of some twelve species in addition to the eight which advectitiously extend to the Carolinas. This area marks for the Tellininae the beginning of the Antillean fauna. Only six species are more or less limited to continental North America.

Over forty-five species of the Western Atlantic Tellininae are distributed in the Antillean Province, and of these, six possess distributions restricted to the Antilles. The remaining species are more widely ranging. The South American fauna, on the East coast of South America from the Guianas to Argentina possesses nineteen species, and of this number only five are endemic. Three of the endemics are strictly southern temperate in their range and are found in the Argentinian Province while the other two are represented by the very poorly known species, *T. brasiliana* and *T. alerta*. The other fourteen South American species are in the Brasilian Subprovince and are all related and derived from the Antillean fauna. Among certain of the latter, some divergences are apparent between northern and southern populations corresponding roughly to populations of Caribbean and Brasilian Subprovinces.

A tally of the number of species geographically shows that the lesser Antilles with thirty-three species is the richest area while southern Florida is next in richness with thirty species. Each of the Greater Antilles has a fauna nearly the same size numerically. Hispaniola and Cuba have twenty-six species. The smaller islands of Jamaica and Puerto Rico each has twenty-two species. Further, it may be remarked that Bermuda has received its thirteen species from the Antillean fauna. In the pattern of distribution for the subfamily, it can be seen that there is an area of concentration in the Antilles and a gradual diminution to the north and south. North America has a richer fauna than South America and the elements of the South American fauna are predominantly Antillean. Such a distribution pattern is analogous to that reported for other molluscan and invertebrate groups (Ekman, 1953).

TABLE I. Distribution of the species of the Tellinidae in the Western Atlantic Ocean.

	Northernmost record	N of Cape Cod	S of Cape Cod-Va.	North Carolina	South Carolina	Georgia	Florida (East)	Florida (South)	Florida (West)	Gulf Coast	Mexico	Central America	Bermuda	Bahama Islands	Cuba	Jamaica	Hispaniola	Puerto Rico	Virgin Islands	Lesser Antilles	Colombia	Venezuela	Guianas	Brasil	Uruguay	Argentina	Southernmost record
radiata	South Carolina				—			—	—		—	—	—	—	—	—	—		—	—		—	—				British Guiana
brasiliana	---																							—			Brasil
iheringi	Mar del Plata																								—	—	San Matias, Argentina
petitiana	Sao Thome, Brasil																							—	—	—	San Matias, Argentina
listeri	off Cape Lookout, N.C.			—		—	—	—	—		—	—	—	—	—	—	—		—		—	—		—			N of Bahia, Brasil
laevigata	Beaufort, N.C.			—				—	—				—	—	—				—	—		—					La Guayra, Venezuela
magna	Fort Walton, Fla.							—	—				—	—	—				—	—							Martinique, West Indies
fausta	Cape Lookout, N.C.			—				—			—	—	—	—	—	—	—	—	—	—	—	—					Aruba, off Venezuela
squamifera	Cape Hatteras, N.C.			—				—	—	—	—																Dry Tortugas, Fla.
persica	Matanzas, Cuba														—			—		—							Tobago, West Indies
americana	Cape Lookout, N.C.			—				—		—										—							Barbados, West Indies
cristallina	Sullivan's Id., S.C.				—							—				—	—	—	—		—	—					Margarita Id., Venezuela
aequistriata	off Beaufort, N.C.			—	—			—	—	—	—	—		—	—	—	—	—	—	—				—			off Bahia, Brasil
alerta	---																							—			type locality only
martinicensis	Tampa, Fla.							—	—			—			—	—	—	—	—	—							Tobago, West Indies
juttingae	Trinidad																			—			—				Surinam
gouldii	Palm Beach, Fla.							—			—		—	—	—		—		—	—		—					Margarita Id., Venezuela
angulosa	Biscayne Bay, Fla.							—	—		—	—			—	—	—	—	—	—		—		—	—		Canelones, Uruguay
alternata	Cape Hatteras, N.C.			—	—	—	—	—	—	—																	Florida Keys
tayloriana	---									—	—	—															Texas
trinitatis	Marco, Fla.								—			—			—								—		—		Canelones, Uruguay
punicea	Belize, B.H.											—				—	—	—	—	—	—	—	—	—			Sao Francisco, Brasil
nitens	Cape Hatteras, N.C.			—				—		—					—	—	—	—		—							Tobago, West Indies
guildingii	Bermuda												—	—	—	—			—	—							Barbados, West Indies
lineata	St. Augustine, Fla.						—	—	—	—	—	—		—	—	—	—	—	—	—	—	—		—			Sao Sebastian, Brasil
vespuciana	off Texas									—		—				—	—	—		—							Trinidad
mera	Lake Worth, Fla.							—	—				—	—	—		—	—	—	—		—					Curacao, West Indies
paramera	Miami, Fla.							—					—	—	—		—			—							Barbados, West Indies
tampaensis	Mosquito Lagoon, Fla.						—	—	—	—				—		—	—										Aquin, Haiti
colorata	St. Thomas, Virgin Ids.																		—	—							Guadeloupe, West Indies
agilis	St. Lawrence R., Canada	—	—	—	—	—																					Sapelo Id., Georgia
texana	Beaufort, N.C.			—	—	—	—	—	—	—	—			—	—												Bahia Honda, Cuba
versicolor	Sakonet, R.I.		—	—	—		—	—	—	—	—	—			—	—	—		—	—							Gulf of Paria, Trinidad
exerythra	Portland Bight, Jamaica											—				—	—	—						—			Brasil
probrina	Miami, Fla.							—		—				—						—							Tobago, West Indies
diantha	Barbados, West Indies																			—			—	—			Rio de Janeiro, Brasil
euvitrea	St. Lucia, Cuba														—		—	—									Ponce, Puerto Rico
tenella	Wareham, Mass.		—	—					—	—																	Horn Id., Mississippi
sybaritica	Beaufort, N.C.			—			—	—	—		—		—	—	—	—	—	—		—				—			Bahia, Brasil
gibber	La Paloma Rocha, Uruguay																								—	—	San Matias, Argentina
similis	Isle of Palms, S.C.				—			—	—		—	—		—	—	—	—	—	—	—							Barbados, West Indies
iris	Cape Hatteras, N.C.			—	—	—	—	—	—	—																	Miami, Fla.
consobrina	Miami, Fla.							—					—		—			—	—	—							Tobago, West Indies
sandix	Jamaica															—	—	—		—				—	—		La Paloma Rocha, Uruguay
candeana	Palm Beach, Fla.							—	—				—	—	—				—	—							Guadeloupe, West Indies
carnaria	Miami, Fla.							—						—	—	—	—	—	—	—				—	—		Mar del Plata, Uruguay
pseudocarnaria	Jamaica											—				—	—	—	—	—	—	—					Guanta, Venezuelas
pisiformis	Bimini, Bahamas							—				—		—	—	—	—	—	—	—	—	—		—			Sao Francisco, Brasil
mirabilis	Cape Hatteras, N.C.			—	—			—	—	—	—		—	—	—		—	—	—	—							Grenada, West Indies
gabbi	Key West, Fla.							—		—		—		—						—	—		—	—			Recife, Brasil
producta	Jamaica											—				—	—	—		—				—			Barra Secca, Brasil
cristata	Beaufort, N.C.			—	—		—	—	—	—																	Progreso, Yucatan

The information accrued from an analysis of the distribution of each species in the subfamily is presented in Tables II and III. It can be seen that patterns of distribution are indicative of the importance of geographic isolation upon the formation of species. Of the fifty-two Western Atlantic species, twenty-six are represented by analogous species in the Eastern Pacific. The Isthmus of Panama has, since its establishment in the Pliocene, acted as an extrinsic barrier in the separation of populations and has thereby influenced the consequent pattern of speciation. Allopatric species-pairs, nominal genera and subgenera like *Phyllodina*, *Laciolina* and *Elliptotellina*, are good examples of superspecies.

TABLE II. Western Atlantic species and their Eastern Pacific Analogs

Western Atlantic	*Eastern Pacific*
listeri	cumingii
laevigata	viridotincta
squamifera	pristiphora
persica	fluctigera
americana	pacifica
cristallina	rhynchoscuta
aequistriata	reclusa
martinicensis	proclivis
juttingae	lyra
angulosa	eburnea
alternata	laceridens
punicea	simulans
nitens	inaequistriata
mera	meropsis
tampaensis	suffusa
exerythra	erythronotus
sybaritica	amianta
gibber	hiberna
iris	virgo
sandix	esmeralda
pseudocarnaria	chroma
pisiformis	panamensis
mirabilis	lenticula
gabbi	disjuncta
producta	ervilia
cristata	burnetti

In Table III, a similar pattern within polytypic groups of the Western Atlantic is evident. Twelve species-pairs, representing nearly 50% of the total number of species are allopatrically distributed. Extrinsic mechanisms of isolation are not as obvious as the definitive features of the Isthmus of Panama but include the limitations of gene flow between allopatric populations imposed by shorter larval periods, adverse current conditions, or larval substrate specificities.

In summation, the pattern of distribution in the Tellininae is consistent with that exhibited by other littoral marine groups, namely that boundaries established by temperature, current, and other hydrographic conditions do delimit geographical ranges at such points as Cape Hatteras, the Straits of Florida, and southern Brasil. In addition, the pattern of distribution within and between species-groups is largely allopatric, that is to say that the nearest relatives of a species are isolated geographically from each other. Such a fact is consonant with, as well as supportive of, the accepted thesis of geographic speciation.

TABLE III. Allopatric species-pairs in the Western Atlantic

sandix	iris
gibber	versicolor
tenella	sybaritica
diantha	probrina
euvitrea	probrina
agilis	texana
juttingae	martinicensis
alerta	aequistriata
angulosa	alternata
alternata	tayloriana
radiata	brasiliana
squamifera	persica

SYSTEMATIC TREATMENT

Family **Tellinidae**

Gills small, posterior, not plicate, the outer demibranch dorsally directed and a reflected lamina obsolete or lacking; labial palps very large, more or less united posteriorly. Byssal apparatus obsolete. Foot compressed, short and not grooved. Mantle margins papillose with a large ventral pedal gap. Siphons long, extensile, separate to their bases and capable of retraction into an extensive pallial sinus. Ligament external, opisthodetic and generally subtended by nymphal callosities. Hinge with two cardinal teeth in each valve; lateral dentition present or absent. Cruciform muscles posterior.

Subfamily **Tellininae**

Shell narrowly or broadly lanceolate to ovate in shape, the posterior side generally shorter and often strongly flexed to the right posteriorly. Valves usually of unequal convexity, the left larger and more convex. Hinge with both cardinal and lateral teeth. Surface sculptured concentrically, sculpture generally heavier on the rostral areas.

KEY TO GENERA AND SUBGENERA OF TELLININAE IN THE WESTERN ATLANTIC

1. External sculpture of shell with flexuous scissulations . . . . *Strigilla*
External sculpture of shell without flexuose scissulations 2

2. Both anterior and posterior dorsal margins spinose . . . . *Tellidora*
Both anterior and posterior dorsal margins not spinose 3

3. Posterior dorsal slope with strong radial sculpture . . . . *Elliptotellina*
Posterior dorsal slope with concentric sculpture 4

4. Surface of disc obliquely grooved with scissulations . . . . *Scissula*
Surface of disc not obliquely grooved with scissulations 5

5. Right anterior lateral tooth proximal or subproximal to the cardinal complex . 6
Right anterior lateral tooth distal to the cardinal complex 9

6. Calcareous element of the ligament greatly thickened and sunken . . . *Laciolina*
Calcareous element of the ligament, if thickened, not sunken 7

7. Pallial sinus obliquely ascending . . . . *Arcopagia*
Pallial sinus not obliquely ascending 8

8. Right posterior lateral tooth strong; supportive rib internally . . . *Eurytellina*
Right posterior lateral tooth weak; internal rib lacking . . . . *Angulus*

9. Shell smooth and polished externally 10
Shell not smooth, with strong concentric sculpture 11

10. Pallial sinus confluent with the pallial line at the base of the anterior adductor muscle scar . . . . *Acorylus*
Pallial sinus confluent with the pallial line posterior to the base of the anterior adductor muscle scar . . . . *Tellina*, s.s.

11. Pallial sinus not connected to the anterior adductor muscle scar by a linear scar . . . . *Merisca*
Pallial sinus connected to the anterior adductor muscle scar by a linear scar . 12

12. Shell strongly flexed to the right posteriorly . . . . *Tellinella*
Shell not strongly flexed to the right posteriorly . . . . *Phyllodina*

Genus **Tellina** *Linnaeus*

Tellina Linnaeus 1758, Systema Naturae, Ed. 10, p. 674 (type species, *Tellina radiata* Linnaeus 1758, subsequent designation Schmidt 1818, p. 51).

Description. Shell small to large, elliptical to ovate in shape, left valve generally more convex than the right, variously flexed to the right posteriorly. Fragile to solid. Concentric sculpture predominant. Hinge with cardinal and lateral dentition. Cardinal teeth two in each valve: in the left valve, the anterior cardinal tooth is bifid and the posterior cardinal tooth is single and laminate; in the right valve, the anterior cardinal tooth is single and laminate and the posterior cardinal tooth is bifid. Lateral dentition variously developed, but lateral teeth of the right valve strong. Pallial sinus variously formed. Shell white to highly colored.

Considerable controversy has reigned over the question of the designation of the type species for the genus *Tellina*. Most early designations, including those of Children (1823, p. 305), Gray (1847, p. 186), and Stoliczka (1870, p. 116), cite *Tellina radiata* Linnaeus as type. In 1900, Dall employed *Tellina virgata* Linnaeus as the type species which was used with reference to Lamarck (1799). Thiele (1935) followed Dall in this usage and recently Olsson (1961) has adopted this designation.

This confusion has arisen in regard to the question of the validity of type species designations by Lamarck. Dodge (1947), quoting a statement from Lamarck's introduction to the Prodrome, has argued that the examples cited by Lamarck represent type designations. In Opinion 79 of the International Rules of Zoological Nomenclature, the examples cited by Lamarck in his Systeme of 1801 are rejected as bonafide type designations (Kennard, Salisbury, and Woodward, 1931). It is possible that this opinion may be extrapolated to the Prodrome of 1799. In the new Code of Zoological Nomenclature (1961), Article 69 (a) (iii) states:

> "In the absence of a prior valid type-designation for a nominal genus, an author is considered to have designated one of the originally included nominal species, if he states that it is the type (or type-species), for whatever reason, right or wrong, and if it is clear that he himself accepts it as a type-species."

Certainly Lamarck did not select a type in the rigidly construed sense since it can be seen that he changed the example under the genus *Tellina* in the 1801 work to *Tellina radiata* Linnaeus. The first type designation of *Tellina* is that of Schmidt (1818) and not that of Children (1823) as some workers have cited. Schmidt tabulated the work of Gmelin, Bruguière, Lamarck, von Mühlfeld and Oken. In the case of Lamarck, he referred to the Systeme of 1801 and thereby cited *Tellina radiata* as type; the genus then is defined as *Tellina* Linnaeus, *sensu* Lamarck 1801.

Subgenus **Tellina** s.s.

Tellina Linnaeus. Lamarck 1801, Systeme Animaux, p. 124 (type species, *Tellina radiata* Linnaeus 1758, subsequent designation Schmidt 1818, p. 51).

Tellinarius Dumeril 1806, Anat. Zool., Index.[1]

Musculus Mörch 1853, Catalogus Conchyliorum Comes di Yoldi, 2: 13 (type species, *Tellina radiata* Linnaeus 1758, monotypy), *non* Röding 1798.

Liotellina Fischer 1887, Manuel Conchyliologie, p. 1147 (type species, *Tellina radiata* Linnaeus 1758, original designation).

Description. Shell of medium to large size, elongate-subelliptical in shape, moderately thick and flexed to the right posteriorly. Sculpture smooth, consisting of fine radial or concentric lines. Lateral dentition strong in the right valve and consisting of a distal anterior and a distal posterior tooth. Laterals of the left valve more or less poorly developed and equidistant from the cardinal complex. Pallial sinus large, extending near to the anterior adductor muscle scar and descending arcuately to the pallial line. The pallial sinus is posteriorly confluent with the pallial line for about half the ventral length.

The problems in the selection of a type species for the genus have been discussed under the generic heading. Schmidt's designation has the effect, as pointed out by Salisbury (1934) of reducing *Tellina* s.s. to a relatively small group or species. The subgenus appears to have attained its highest development in the Western Atlantic. The peculiarly twisted *Tellina chariessa* Salisbury (=*elegans* Gray) represents the group in the Indo-Pacific, and *Tellina* s.s. is conspicuously absent from the Eastern Pacific.

KEY TO THE SPECIES OF TELLINA s.s. IN THE WESTERN ATLANTIC

1.	Shell large, exceeding 45 mm. in adult length; some red coloration	2
	Shell small, less than 45 mm. in adult length; no red coloration	3
2.	Internally, shell white with rays or suffusions of yellow orange or red	*radiata*
	Internally, deep red purple	*brasiliana*
3.	Periostracum golden-brown: shell solid	*iheringi*
	Periostracum olivaceous green; shell thin	*petitiana*

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[1] As Dall, Bartsch and Rehder (1938) point out *Tellinarius* Dumeril was used as an exact definition of *Tellina* Linnaeus and therefore becomes an absolute synonym for *Tellina* s.s.

Tellina (Tellina) radiata *Linnaeus*

Plate 129; figs. 1–4; Plate 130, fig. 1

Tellina radiata Linnaeus 1758, Systema Naturae, Ed. 10, p. 675 (In Oceano Europaeo) [type locality, here corrected and restricted, Montego Bay, Jamaica; type specimens, in collection of Linnean Society, London].

Tellina unimaculata Lamarck 1818, Animaux s. Vertebres, **5**: 521 (l'Ocean d'Amerique) [type locality, here restricted, Montego Bay, Jamaica; syntypes, Museum d'Histoire Naturelle, Geneva].

Tellina (Musculus) radiata Linnaeus. Mörch 1853, Catalogus Conchyliorum Comes di Yoldi, **2**: 13.

Tellina (Tellina) radiata Linnaeus. H. and A. Adams 1856, Genera Recent Mollusca, **2**: 394.

Tellina (Eutellina; Liotellina) radiata Linnaeus. Fischer 1887, Manuel Conchyliologie, p. 1147.

Description. Shell extending to 114 mm. (about 4½ inches) in length and to 53 mm. (about 2¼ inches) in height, elongate-elliptical, solid, moderately tumid, with the left valve more convex and with a weak flexure to the right posteriorly. Umbos subcentral and slightly inflated. Anterior margin smoothly rounded; ventral margin straight and with a marked postbasal constriction; posterior dorsal margin gently sloping and long; posterior margin short and forming a sloping truncation. Sculpture consisting of evenly spaced obsolete concentric lines; fine radial lirations intersect the concentric lines and produce a microscopic cancellate pattern. Ligament dark brown and protuberant. Calcareous element of the ligament subtended by nymphal callosities. In the left valve, the cardinal complex consists of an anterior strong bifid tooth whose anterior lobe is larger and of a posterior thin laminate tooth; the lateral teeth are both distal to the cardinal complex and weak or obsolete. In the right valve, the cardinal complex consists of a posterior strong bifid tooth with equal lobes and of an anterior strong but thin laminate tooth; the lateral teeth are both distal to the cardinal complex, but extremely well developed and strong. An internal strong supportive ridge radiates from the umbonal region toward the anterior adductor muscle scar. Adductor muscle scars well impressed. Pallial sinus nearly contiguous with the anterior adductor scar, more or less linguiform, not rising above the adductor scars and confluent with the pallial line for about one half its ventral length. Externally the color of the shell varies from pure white to alternating

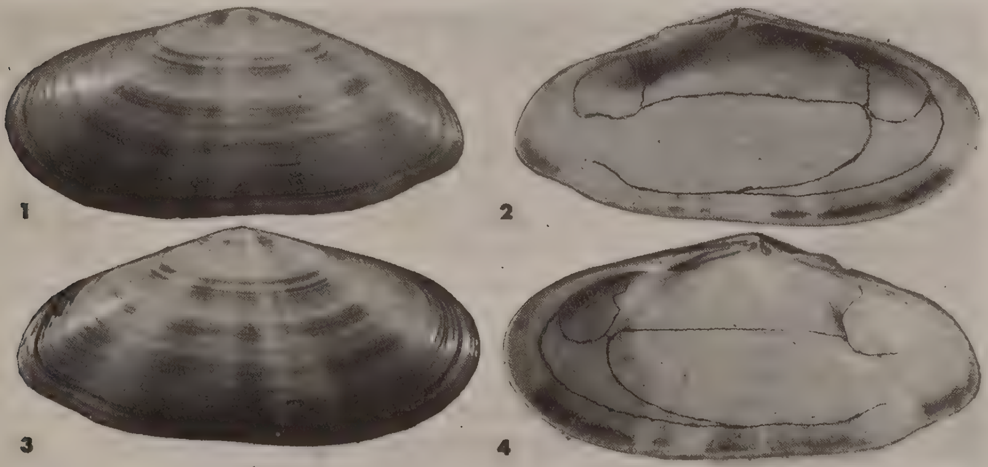

Plate 129. *Tellina radiata* Linnaeus. Fig. 1. External view of the left valve. Fig. 2. Internal view of the left valve. Fig. 3. External view of the right valve. Fig. 4. Internal view of the right valve. Great Abaco Island, Bahamas, USNM 73109 (about 1x) [L=70.2 mm.]. L=length

rays of red and pink which broaden peripherally. Internally, the shell may be suffused with pale yellow or red.

length	height	width	
88.0 mm.	41.0 mm	24.0 mm.	Syntype of *radiata* Linnaeus
86.0	42.0	20.0	Syntype of *unimaculata* Lamarck
114.0	53.0	28.5	Cat Island, Bahamas
64.0	32.0	16.5	Tortola, Virgin Islands
19.0	9.0	4.2	Great Inagua, Bahamas

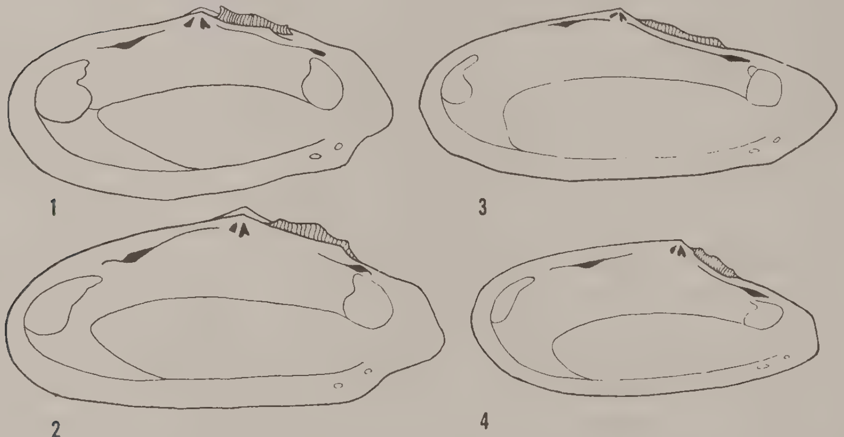

Plate 130. Figs. 1–4. Diagrammatic illustration of the internal surface of the right valve showing the dental configuration and muscle scars. Fig. 1. *Tellina radiata* Linnaeus (about 1.2x) [L=50 mm.]. Fig. 2. *Tellina brasiliana* Spengler (about 1.4x) [L=50 mm.]. Fig. 3. *Tellina petitiana* d'Orbigny (about 2x) [L=33 mm.]. Fig. 4. *Tellina iheringi* Dall (about 1.7x) [L=30 mm.].

Remarks. This species may be considered one of the more successful species of *Tellina* in the Western Atlantic. Of a subtropical to tropical range, it seems to have a central, most concentrated population in the Bahamas.

In a series of individuals from the same locality, a continuum in the stages of growth and development may be observed. An allometric pattern is definitely evident when smaller and younger individuals are contrasted with larger and older ones. In the smaller individuals, the anterior dorsal margin is more elongate, more smoothly and gently sloping than in adults; this margin occupies a larger percentage of the total length as well. The nymphal callosity and the calcareous layer of the ligament are most often equal in length, but the total length of each of these structures varies in individuals according to age. In general, older individuals which possess heavier and larger shells also have a longer nymph. The posterior indented arcuation of the ventral margin also increases in strength with age.

The characters which are most variable are the color and the color pattern of the shell. Lamarck (1818) named the white rayless form, *unimaculata.* White individuals of *radiata* reflect the polymorphic nature of the species and are found in nearly all populations regardless of geographical distribution. Some kind of radial pattern of red seems to be the general configuration of external coloration. The same generalization is true of the pattern and coloration on the internal surface of the valves, but in addition, yellow coloration seems to be stronger and more intensely concentrated in the central disc area of the internal surface. More often than not, there is a concentration of red on the umbonal region of the shell even in those individuals that are predominantly white.

This species is an inhabitant of the shallow slope waters, and Robertson (59) has indicated that it is a typical representative of the offshore sand community. Abbott (1958) described its habitat preferences in Grand Cayman; in this locality, *radiata* occurred in clear sand at depths between 6 and 48 feet; it seemed to prefer fairly clear ocean water and was not found in the warm inshore shallows.

The fossil record of this species is incomplete; it is known to occur in the Pleistocene (Rehder, 1962). The closest relative of *T. radiata* in the Western Atlantic is *T. brasiliana* Spengler. In the Indo-Pacific, *Tellina chariessa* Salisbury is similar to *radiata*, but the former is asymmetrically twisted.

Range. Tellina radiata occurs from Lake Worth, Florida south through the Greater and Lesser Antilles to the Guianas in South America.

Specimens examined. FLORIDA: Lake Worth; Pompano (both MCZ); Fort Lauderdale (ANSP); Miami (USNM); Key Biscayne; Virginia Key; Hawks Channel, Garden Cove, Key Largo, in 2 fathoms (all MCZ); Conch Key, in 1–5 feet (USNM); Grassy Key (ANSP); Key Vaca; Bahia Honda Key (both MCZ); Key West; Loggerhead Key, Tortugas (both USNM); Sanibel (USNM; CNM); Boca Grande, Gasparilla Island (ANSP); Paradise Beach, Hog Island (ANSP); Cedar Keys (USNM; MCZ). MEXICO: 15 miles N of Tecolutla, Veracruz (MCZ); Campeche (ANSP); Progreso; Cabo Catoche (both MCZ); Cozumel Island (ANSP). BRITISH HONDURAS: Belize (MCZ); St. Georges Cay (USNM). HONDURAS: Utilla Island (USNM). BERMUDA: Castle Roads, Castle Harbour, in 4–5 fathoms (MCZ); off Nonesuch, in 15 feet (USNM); Long Beach, Warwick (MCZ). BAHAMAS: Cay Sal; Alicetown, North Bimini (both MCZ); Nixon's Harbour, South Bimini; Gun Cay (both ANSP); Dollar Harbour, South Cat Cay; West End, Wood Cay, Eight Mile Rock, Hawksville Creek, Holmes Cay, Sweetings Cay, and Freetown, Grand Bahama; Green Turtle Key, Tilloo Cut, and Marsh Harbour, Great Abaco (all MCZ); Mintie Bar, Andros (USNM); North Cay, Nassau Harbour, Dick's Point, Fox Hill, Culbert Point, North Cay, Adelaide, Old Fort and Lake Cunningham, New Providence; Governor's Harbour and Sandy Point, Eleuthera; Arthurstown, North End Point, Russell Creek, Orange Creek, Campdown and Landing Rock, Cat Island; Little San Salvador Island; Stocking Island, Great Exuma; Watlings Island; Cockburntown, San Salvador; Simms, Cape St. Marie, and Clarence Town, Long Island (all MCZ); Lobos Island; Rocky Point, Crooked Island (both USNM); Fortune Island; Atwood's Cay; Abraham's Bay, Mariguana Island; Turks Island; Matthew Town, Great Inagua (all MCZ). CUBA: Cape San Antonio; Cape Cajon; Cayo Levisa (all USNM); Habana; Pueblo Nuevo, Matanzas (both MCZ); Cayo Galindo, Cardenas (CNM); Cayo Cristo, Sagua la Grande, La Sortija, Cayo Caiman and Cayo Frances, Las Villas; Cayo Maja Figuro, Camagüey; Punta de los Colorados, Cienfuegos Bay (all MCZ); 20 miles W of Santiago (USNM). JAMAICA: Montego Bay (USNM); Portland Point; Middle Cay, Pedro Bank (both MCZ). HISPANIOLA. HAITI: Baie des Flamands; Les Sept Freres Islands (both USNM). SANTO DOMINGO: Monte Cristi; Puerto Plata (both MCZ). VIRGIN ISLANDS: Anegada Island (ANSP); Devil's Bay, Virgin Gorda; Tortola; Guana Island; Cancel Bay, St.

John: Bird Key, St. Thomas; Sandy Point, St. Croix (all MCZ). LESSER ANTILLES: St. Martins (ANSP); St. Kitts (MCZ); Nevis (ANSP); Falmouth Harbour, Antigua, in 3–6 fathoms (USNM); Guadeloupe; Barbados (both ANSP). CARIBBEAN ISLANDS: Georgetown, Low Point, West Bay and Little Bluff, Grand Cayman (all ANSP). Swan Island; Curaçao (both MCZ). VENEZUELA: La Guayra; Orchilla Island (both USNM). BRITISH GUIANA: SE coast of British Guiana (ANSP).

Tellina (Tellina) brasiliana *Spengler*

Plate 130, fig. 2; Plate 131, fig. 1

Tellina brasiliana Spengler 1798, Skrivter Naturhistorie Selskabet, **4**(2): 94, pl. 12, fig. 4 (Fra Brazilien), *non* Lamarck 1818 [type locality, here restricted, Praia de Itapoan, Bahia, Brasil; holotype, Zoological Museum, Copenhagen].

Tellina semizonalis Lamarck 1818, Animaux s. Vertebres, **5**: 521 (no locality given); Delessert, 1841, pl. 6, fig. 1 [type locality, here restricted, Praia de Itapoan, Bahia, Brasil; holotype, Museum d'Histoire Naturelle, Geneva].

Tellina (*Tellina*) *brasiliana* Spengler. H. and A. Adams 1856, Genera Recent Mollusca, **2**: 394.

Tellina (*Musculus*) *brasiliana* Spengler. Römer 1870, Conchilien-Cabinet (2), **10**(4): 9, pl. 5, figs. 1–3.

Description. Shell extending to 103 mm. (about 4 inches) in length and to 50.5 mm. (about 2 inches) in height, elongate-lanceolate, solid, with the left valve more convex and with a strong flexure to the right posteriorly. Umbos slightly posterior to the middle and pointed. Anterior margin very narrowly rounded; ventral margin straight and with a slight indented arcuation behind; anterior dorsal margin rather long and straight; posterior dorsal margin gently descending and straight; posterior margin slightly convex and forming a short oblique posterior truncation. Sculpture consisting of weak, evenly spaced concentric lines; radial lirae present. Ligament dark brown and protuberant. Calcareous element subtended by a thickened nymphal callosity. In the left valve, the cardinal complex consists of an interior thickened, strong bifid tooth whose anterior lobe is larger and of a posterior thin laminate tooth; the lateral teeth are both distal to the cardinal complex and quite weak or obsolete. In the right valve, the cardinal complex consists of a posterior strong bifid with subequal lobes and of an anterior strong but thin laminate tooth; the lateral teeth are both distal to the cardinal complex but extremely well developed and strong. Adductor muscle scars moderately well impressed; pallial sinus rises slightly behind, is slightly convex above and falls to the pallial line in a position beneath the umbos. The sinus extends to, but does not coalesce with the anterior adductor muscle scar. Externally the shell is polished and white with a purplish tinge and may appear banded with red and purple; internally the shell is polished and purple with a white periphery.

length	height	width	
103.0 mm.	50.5 mm.	33.0 mm.	Holotype of *brasiliana* Spengler
45.0	21.0	9.0	Holotype of *semizonalis* Lamarck
78.0	39.0	—	Brasil
52.0	22.0	—	Praia de Itapoan, Brasil

Remarks. The status of this species has been somewhat controversial, due in part to its rare occurrence. The nearest relative of *Tellina brasiliana* is the very common West Indian species, *T. radiata*. The distributions of the present species are allopatric and indicative of a geographical separation of the ancestral populations. The most spectacular difference between *brasiliana* and *radiata* is the color of the shell. *Tellina brasiliana* possesses a purple interior and a variously rayed and banded exterior whereas *radiata* varies between a pure white shell and one which is rayed externally and internally with red, yellow or orange. Furthermore, the posterior flexure to the right, the radial lirae, the curvature of the right valve and the posterior internal ribs and rays are all stronger in *brasiliana*. Other important and diagnostic traits include the closely set, strongly incised, and parallel sculpture along the posterior slope in *brasiliana*.

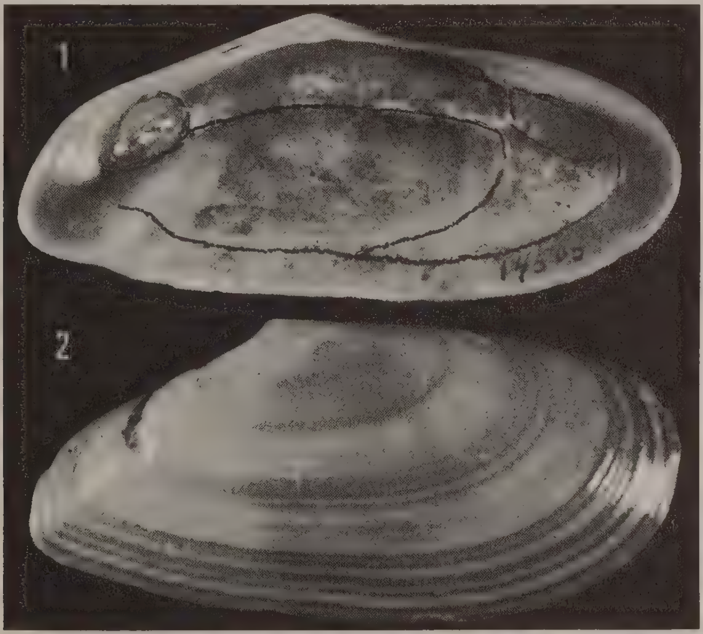

Plate 131. Fig. 1. *Tellina brasiliana* Spengler. Internal view of the left valve, Praia de Itapoan, Brasil, MCZ 145057 (about 2.2x) [L=52 mm.]. Fig. 2. *Tellina iheringi* Dall, external view of the right valve, Golfo San Matias, Argentina, MCZ 145058 (about 3x) [L=31.5 mm.].

Range. The distribution of this species seems to be wholly confined to the coast line of Brasil. Oliveira in an unpublished manuscript has given the single locality of Ceará (Fortaleza) for this species. The only other known specific locality is the Praia de Itapoan at Bahia.

Specimens examined. Brasil: (BMNH; ZMK); Praia de Itapoan, Estado do Bahia (MCZ).

Tellina (Tellina) iheringi *Dall*

Plate 130, fig. 4; Plate 131, fig. 2

Tellina (*Liotellina*) *iheringi* Dall 1900, Proc. U.S. Nat. Mus., **23**: 311, fig. 2 (type locality, *Albatross I* station 2765, off Rio de la Plata, in 10½ fathoms [18 miles NE of Punta Mendanos, 36°43′ S; 56°23′ W]; holotype, USNM, no. 108531).

Description. Shell extending to 35.5 mm. (about 1¼ inches) in length and to 17.5 mm. (about ⅝ inches) in height, elongate, subsolid, with the right valve only slightly more convex and with a weak posterior flexure to the right. Umbos posterior to the middle and blunt. Anterior margin narrowly rounded; ventral margin convex and gently rising posteriorly; anterior dorsal margin long and gently sloping; posterior dorsal margin gently sloping and slightly concave; posterior margin short and forming an ill-defined truncation. Concentric sculpture absent or consisting of weak lirations which are strongest on the posterior slope; radial vermiculations which broaden peripherally occur on the disc. Ligament short and deeply set. Calcareous element subtended by an elevated nymphal callosity. In the left valve, the cardinal complex consists of an anterior strong deltoid bifid tooth with subequal lobes and of a posterior weak, very long and thin laminate tooth; anterior lateral tooth distal and very weak; posterior lateral tooth distal, poorly developed, but stronger than the anterior lateral tooth. In the right valve, the cardinal complex consists of a posterior strong bifid tooth with subequal lobes and of an anterior thickened laminate tooth; the anterior lateral tooth distal, elongate and strong; the posterior lateral tooth distal and smaller than the anterior lateral; both lateral teeth socketed. Adductor muscle scars rather poorly impressed. Anterior adductor scar elongate, narrow and rounded below; posterior adductor rounded. Pallial sinus equal in both valves, slightly convex above and falling in a sharp arcuation to the pallial line. The pallial sinus is widely separated from the anterior adductor scar. The shell is polished and white, covered externally by a yellowish brown periostracum, which shows darker concentric bands. Internal surface white, polished and shining.

length	height	width	
27.0 mm.	13.0 mm.	5.5 mm.	Holotype of *iheringi* Dall
35.5	17.5	8.0	Punta Norte, Golfo San Matias
31.5	14.0	6.5	Punta Bermeja, Golfo San Matias
24.4	11.3	4.2	Montevideo, Uruguay

Remarks. Tellina iheringi is allied to *Tellina petitiana* and both of these species are more or less restricted to the continental slope fauna of southeastern South America. The close relationship of these species is expressed in a similarity of general characteristics. *Tellina iheringi* is more tumid or inflated than *T. petitiana.* There is a difference in the basic proportions of the shells and this is most easily discerned in the nature of the posterior dorsal slope. In *petitiana*, this margin drops off very sharply from the umbonal area whereas in *iheringi* there is only a gentle inclination with little indication of concavity. The valve thickness of *iheringi* is greater and the periostracum is of a yellowish brown coloration in contrast to the gray-green color exhibited by *petitiana.*

Range. This species is more or less restricted to the coast of Argentina at depths between 7 and 30 fathoms in sandy substrate; its northernmost record is off Montevideo, Uruguay and its southernmost, off Punta Bermeja, Argentina.

Specimens examined. URUGUAY: *Hassler* station, 8 miles SE of Montevideo (31°12′ S; 55°30′ W) in 7 fathoms (MCZ). ARGENTINA: *Albatross I* station 2764, 19 miles NE of Punta Mendanos (36°42′ S; 56°23′ W), in 11.5 fathoms; *Albatross I* station 2765, 18 miles NE of Punta Mendanos (36°43′ S; 56°23′ W), in 10.5 fathoms (both USNM); *Hassler* station, 17 miles NNE of Punta Rasa (40°22′ S; 60°35′ W), in 30 fathoms; *Hassler* station, off Bahia Rosas, Golfo San Matias (41°15′ S; 63°50′ W), in 25 fathoms;

Hassler station, off Punta Bermeja, Golfo San Matias (41°17′ S; 63°00′ W), in 17 fathoms (all MCZ).

Tellina (Tellina) petitiana *d'Orbigny*

Plate 130, fig. 3; Plate 132

Tellina petitiana d'Orbigny 1846, Voyage Amer. Cent., p. 537, n. 540, pl. 81, figs. 26–27 (au large du cap Saint-Thomé, sur la côte du Brésil) [holotype, BMNH, no. 54.12.4.696].

Tellina petitiana d'Orbigny. Smith 1915, Terra Nova Reports, Mollusca, Pt. 1, p. 101.

Description. Shell extending to 45 mm. (about $1\frac{3}{4}$ inches) in length and to 23 mm. (about 1 inch in height, elongate, lanceolate posteriorly, thin, fragile, compressed, with the right valve slightly more convex than the left and with a weak posterior flexure to the right. Umbos central and pointed. Anterior margin broadly rounded; ventral margin straight and rising in a postbasal arcuation; anterior dorsal margin long and slightly convex; posterior dorsal margin long and gently sloping. Sculpture consisting of closely set, weak concentric lirations; radial sculpture consisting of extremely fine vermiculations on the disc which broaden peripherally. Posterior ridge and sulcus present. Ligament dark brown and not protuberant. Calcareous element of the ligament not strongly developed and subtended by very weak nymphal callosities. In the left valve, the cardinal complex consists of an anterior deltoid bifid tooth with subequal lobes and of a posterior elongate, laminate tooth; anterior and posterior lateral teeth absent or obsolete, consisting of distal thickening of the hinge plate. In the right valve. the cardinal complex consists of a posterior subdeltoid bifid tooth whose anterior lobe is larger and of an anterior, divergent thickened laminate tooth; anterior lateral tooth subproximal, long, thin and rather fragile; the posterior lateral tooth distal and elongate; both laterals socketed. Adductor muscle scars moderately well impressed. The anterior adductor somewhat elongate but rounded below; the posterior adductor irregularly rounded. Pallial sinus equal in both valves, rising only slightly above the base of the posterior adductor, irregularly flattened above and descending in a smooth broad arcuation to the pallial line. The pallial sinus is widely removed from the anterior adductor scar. Shell

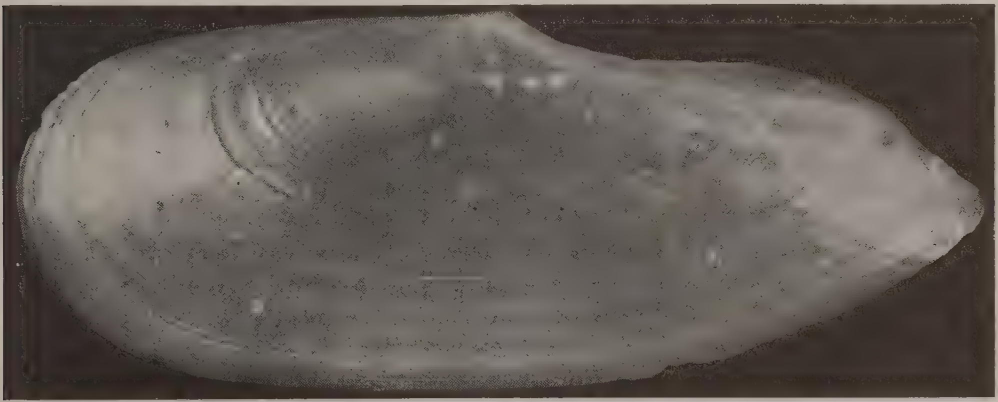

Plate 132. *Tellina petitiana* d'Orbigny, external view of the left valve of the holotype, São Tomé, Brasil, BMNH (about 3.8x) [L=38 mm.].

predominantly white, covered by a thin olivaceous periostracum which often adheres peripherally; rarely iridescent. Internally, white, shining, but not polished.

length	height	width	
38.0 mm.	14.8 mm.	2.3 mm.	Holotype of *petitiana* d'Orb.
45.0	23.0	7.0	San Antonio, Argentina
28.5	11.5	3.5	La Paloma Rocha, Uruguay
12.0	6.0	—	off Montevideo, Uruguay

Remarks. Tellina petitiana appears to be most closely related to *Tellina iheringi;* both species inhabit a similar area off the coast of southern South America. From *iheringi, petitiana* may be distinguished by its thinner and more fragile shell, its lateral compression and its predominantly gray-green periostracum. The posterior dorsal slope in *petitiana* falls sharply from the umbonal region and is more convex and longer than the same margin in *iheringi.* In addition, the posterior slope of *petitiana* is demarcated by a superficial ridge or a number of ridges.

It may appear that the relationship of this species with other members of the subgenus *Tellina* is somewhat distant, because the shell lacks the bright coloration and thickness so typical of *Tellina radiata;* however, the smoothness of the sculpture, the configuration of the pallial sinus and the position of the right lateral dentition serve to justify its subgeneric placement.

Range. The northernmost record is the type locality at Cape São Tomé, in Estado do Rio de Janeiro, Brasil; the species ranges south from this locality to the Golfo de San Matias in Argentina. Depth records show that this species occurs between seven and forty fathoms.

Specimens examined. Brasil: São Tomé (BMNH); Rio de Janeiro (E. A. Smith). Uruguay: La Paloma Rocha (E. Duarte); *Hassler* station, 8 miles SE of Montevideo (31°12′ S; 55°30′ W), in 7 fathoms (MCZ). Argentina: *Hassler* station, Port San Antonio, Golfo San Matias; *Hassler* station, off Bahia Rosas, Golfo San Matias (41°15′ S; 63°50′ W), in 25 fathoms (both MCZ).

Subgenus **Tellinella** *Mörch*

Tellinella Mörch 1853, Catalogus Conchyliorum Comes di Yoldi, **2:** 13 (type species, *Tellina virgata* Linnaeus 1758, subsequent designation, Stoliczka 1870, p. 116[1]).

Telinella Mörch. H. and A. Adams 1856, Genera Recent Mollusca, **2:** 394, error for *Tellinella.*

Eutellina Fischer 1887, Manuel de Conchyliologie, p. 1147 (type species, *Tellina virgata* Linnaeus 1758, original designation).

Tellinarius 'Froriep' Salisbury 1934, Proc. Mal. Soc. London, **21:** 78 and 90 (type species, *Tellina virgata* Linnaeus 1758, original designation), *non* Dumeril 1806.

Description. Shell medium to large size, ovate, elongate or elliptical in outline, solid to subsolid, generally equivalve and nearly equilateral, more or less flexed to the right posteriorly. Concentric sculpture developed, strong and often squamose posteriorly; radial sculpture rare. Lateral dentition developed in both valves. In the right valve, both lateral teeth are distal to the cardinal complex and strongly developed. In the left valve, both lateral teeth are distal to the cardinal complex and moderately developed. Ligament generally strong with subtending nymphal callosities. Pallial sinus linguiform and removed from the anterior adductor muscle scar; confluences of the pallial sinus and pallial line short and limited to the posterior half of the shell.

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[1] The type species is not *Tellina antonii* Philippi as indicated by Salisbury (1934), for Mörch did not cite any type species in his use of the name *Tellinella;* the first known designation was made by Stoliczka.

The subgenus is particularly well represented in the Indo-Pacific where the type, *Tellina virgata* Linnaeus, appears to be widespread. The subgenus is tropical to subtropical in its distribution with a single representative in the Western Atlantic and two species in the Eastern Pacific. Stoliczka (1870) has documented the occurrence of the group in the Cretaceous of India. The subgenus also appears to be well established in the Eocene of Europe and North America.

Tellina (Tellinella) listeri *Röding*

Plate 133, figs. 1–3; Plate 134, fig. 1

Tellina listeri Röding 1798, Museum Boltenianum, p. 185 (West Indies) [type locality, here restricted, St. Kitts; types not seen], *non* Hanley 1844.

Tellina interrupta Wood 1815, General Conchology, p. 146, pl. 36, fig. 3 (Indian and American Seas) [type locality, here restricted, St. Kitts; types lost].

Tellina maculosa Lamarck 1818, Animaux s. Vertèbres, **5:** 521 (Indian Seas) [type locality, here restricted, St. Kitts; syntypes, Museum d'Histoire Naturelle, Geneva].

Tellina mexicana Petit 1841, Revue Zoologique, Societé Cuvier, **4:** 183 (coast of Mexico at Veracruz) [syntypes, Museum d'Histoire Naturelle, Paris].

Tellina (Tellinella) listeri Röding. Mörch 1853, Catalogus Conchyliorum Comes di Yoldi, **2:** 13.

Tellina antoni 'Philippi' Krebs 1864, The West-Indian Marine Shells, p. 100, *antonii non* Philippi 1844.

Tellina (Tellina) interrupta Wood. Dall 1900, Proc. U.S. Nat. Mus., **23:** 293.

Description. Shell extending to 79 mm. (about 2¾ inches) in length to about 41 mm. (about 1½ inches) in height, elongate, solid, somewhat inflated with the left valve slightly more convex and with a very sharp posterior flexure to the right. Umbos central and pointed. Anterior margin narrowly rounded; ventral margin broadly arcuate; anterior dorsal margin long and gently sloping; posterior dorsal margin elongate and straight; posterior margin irregular, divided into two short portions which are more or less oblique to the dorso-ventral axis. Sculpture consisting of strong concentric ridges, separated by well incised sulci; the concentric ridges are stronger along the posterior slope. Rarely radial lirations occur and form a cancellate pattern. Two strong posterior ridges extend from the umbo to the posterior margin in the right valve. Ligament dark brown, strong and protuberant. Calcareous portion of the ligament subtended by thickened nymphal callosities. In the left valve, the cardinal complex consists of an anterior strong bifid tooth with subequal lobes and of a posterior thin laminate tooth; anterior and posterior lateral teeth rather small and equidistant from the cardinal complex. In the right valve, the cardinal complex consists of a posterior strong slightly skewed bifid tooth whose anterior lobe is the larger and of an anterior slightly thickened laminate tooth; the anterior and posterior lateral teeth distal, well developed and socketed above. Adductor muscle scars well impressed. Posterior adductor scar subquadrate; anterior adductor scar subovate. Pallial sinus rising gently posteriorly, broadly convex above, extending toward the anterior adductor muscle scar but well separated from it; the sinus falls obliquely to the pallial line and the confluence is short; a small linear scar often unites the pallial sinus and the anterior adductor scar. Externally, the shell is white to purplish, rarely suffused with yellow and vermiculated with chevrons of purple or brown. Internally, the shell is shining but not polished, white, rarely purple and often suffused centrally with yellow.

length	height	width	
79 mm.	41 mm.	22 mm.	Cayo Frances, Caibarién, Cuba
66	36	18	Cat Island, Bahama Islands
53	27	13	Lake Worth, Florida
14	6	4	Anegada Island, Virgin Islands

Remarks. Variation in *Tellina listeri* is considerable and accounts for the lengthy synonymy. The proportions of individuals vary greatly. Small, immature or young individuals tend to be more narrowly elongate than adults. There is evidence for allometric differences where young stages are of a lower height-length ratio than adults. The strength of both concentric and radial sculpture is also variable. Individuals with strong

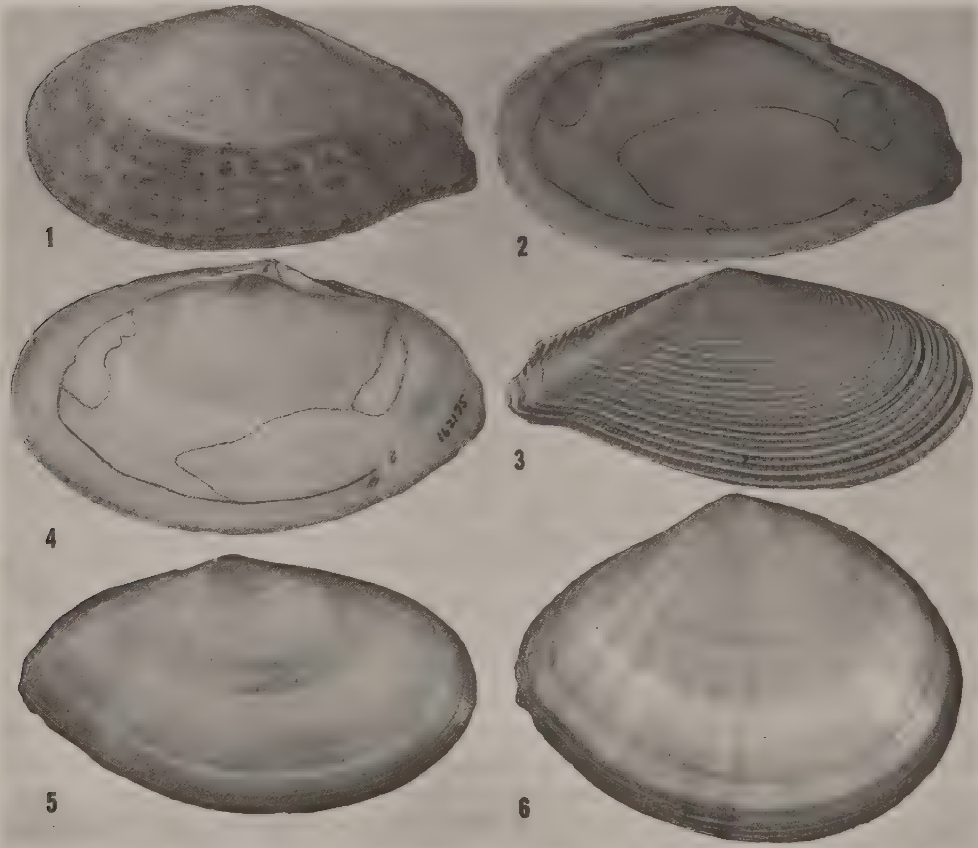

Plate 133. Figs. 1–3. *Tellina listeri* Röding. Fig. 1. External view of the left valve. Fig. 2. Internal view of the right valve, Jamaica, MCZ 155663 (about 1.3x) [L=56 mm.]. Fig. 3. External view of the right valve, Sanibel Island, Florida, MCZ 13503 (about 2x) [L=37 mm.]. Figs. 4–5. *Tellina magna* Spengler. Fig. 4. Internal view of the right valve. Fig. 5. External view of the right valve, Pass-a-grille Beach, Florida (about 0.8x) [L=86 mm. Fig. 6. *Tellina laevigata* Linnaeus, external view of the right valve, Abbott's Cliff, Bermuda, MCZ 218421 (about 1.3x) [L=53 mm.].

concentric lamellae may possess only weakly developed radial lirations whereas some specimens have strong sculpture of both the radial and concentric types. Radial sculpture may be developed posteriorly more than it is anteriorly. The color of *listeri* is its most variable characteristic. Pure white individuals are less rare than pure purple specimens. In general, the external surface of the valves is colored with purple or brown. Internally the valves are generally white with a suffusion of yellow; however, individuals with dark purple interiors also occur.

Tellina listeri is very closely related to *Tellina cumingii* Hanley of the Eastern Pacific. The differences between *listeri* and *cumingii* are often matters of degree wherein some individuals of either species remain virtually indistinguishable. In general, populations of *listeri* have more individuals which have higher and larger shells and fewer individuals with serrated or squamous posterior ridges. In *cumingii*, the shell tends to be narrowly elongate and most specimens are rayed with purple. True *Tellina antonii* is a close relative of *T. listeri* and has been reported from St. Helena by Smith (1890), but specimens of this species though very close to *T. listeri*, appear to be predominantly purple in color.

The precursors of *Tellina listeri* first appear in the Eocene of Vicksburg, Alabama. Dall (1900b), Mansfield (1938) and Gardner (1928) have described related forms from the Oligocene and Miocene of Florida. Olsson and Harbison (1953) have recorded the occurrence of the *T. mexicana* from the Pliocene of Florida, and *T. listeri* has been found in Pleistocene strata in Cuba, Grand Cayman Island, and Brasil.

Tellina listeri appears to be characteristic of offshore, coarse sandy substrates. The species lives in depths from one to fifty fathoms and Abbott (1958) found the species limited to sand substrates between six and forty-eight feet in Grand Cayman.

Range. *Tellina listeri* occurs from Cape Lookout, North Carolina and Bermuda through the Bahamas, the Antilles, the Gulf of Mexico and Caribbean Sea to off the coast of Brasil in the vicinity of Bahia.

Specimens examined. North Carolina: *Albatross I* station 2607, 18 miles E of Cape Lookout (34°38′ N; 76°12′ W), in 18 fathoms; *Albatross I* station 2608, 17 miles ESE of Cape Lookout (34°32′ N; 76°12′ W), in 22 fathoms; *Albatross I* station 2610, 27 miles SE of Cape Lookout (34°20′ N; 76°12′ W), in 22 fathoms; *Albatross I* station 2616, 25 miles SE of Cape Fear (33°42′ N; 71°31′ W), in 17 fathoms; *Albatross I* station 2617, 25 miles SE of Cape Fear (33°37′ N; 77°36′ W), in 14 fathoms; *Albatross I* station 2615, 31 miles ESE of Cape Fear (33°45′ N; 77°25′ W), in 18 fathoms; *Albatross I* station 2619, 37 miles SE of Cape Fear (33°38′ N; 77°36′ W), in 15 fathoms; *Fish Hawk* station 7965, 22 miles SSE of New River Inlet (34°14′ N; 77°05′ W), in 14.5 fathoms (all USNM). Georgia: *Pelican* station 178-14, 63 miles E of Altamaha Island (USNM). Florida: *Pelican* station 172-4, 23 miles NE of New Smyrna, in 14 fathoms; *Pelican* station 172-3, 17 miles E of Daytona Beach (both USNM); South Inlet, Lake Worth in 2–3 fathoms; off Palm Beach in 130 fathoms (both MCZ); off Miami in 6-30 fathoms; Hawk Channel, in 3–4 fathoms; off Fowey Light in 6–45 fathoms; off Long Reef in 38 fathoms (all USNM); off Carysfort Reef, Key Largo in 66–117 fathoms (MCZ); Pepper Fish Key in 9 fathoms (USNM); Grassy Key (ANSP); Key Vaca; Sombrero Key; Looe Key; Boca Chica Key (all MCZ); Key West; Tortugas (both USNM); Naples; Sanibel; Boca Grande, Gasparilla Island (all ANSP); off

Longboat Pass (USNM); Egmont Key; Clearwater Harbor; Madeira Beach Treasure Island (all ANSP); off Anclote Key (USNM); Fort Walton (ANSP); Destin (ANSP; MCZ). Mexico: Veracruz; Isla del Carmen, Campeche; Isla Mujeres, Yucatan (all MCZ). British Honduras: Belize (MCZ). Nicaragua: (ANSP). Panama: off Panama City (USNM). Bermuda: Castle Harbor (MCZ); Truck Island, Harrington Sound (USNM); Grace Island (ANSP). Bahama Islands: West End, Wood Cay, Hawksbill Creek and Holmes Cay, Grand Bahama Island (all MCZ); Marsh Harbour and Sandy Point, Great Abaco; North and South Bimini Islands; Adelaide, Dick's Point and Foxhill, New Providence; off Mintie Bar, SE of South Bight, Andros; Governor's Harbour and Tarpum Bay, Eleuthera; Arthurstown and Orange Creek, Cat Island; Little San Salvador (all MCZ); Rum Cay (USNM); Clarence Town, Cape St. Maria, and Simms, Long Island (all MCZ); NE Point and Abraham's Bay. Mariguana (both MCZ); Matthew Town, Alfred Island, and Mangle Bush, Great Inagua (all MCZ); Lobos Island (USNM). Cuba: *Barrera* station 224, Cape San Antonio; *Barrera* station 211, Cape Cajon; *Barrera* station 209, Santa Rosa, in 3–6 fathoms; *Barrera* station 218, Cayo Hutia Reef; *Barrera* station 208, Bahía Honda, in 1–12 fathoms; *Barrera* station 202, Cabanas Harbor, in 25 fathoms (all USNM); La Chorrera, Habana (USNM; MCZ); Veradero Beach, Matanzas (USNM; MCZ); Cayo Cruz, Cayo Bubas, and Comacho Beach, Cardenas (all CNM); Punta de los Colorados, Cienfuegos Bay; Cayo Frances, Caibarién; Leeward Point and Fish Point, Guantánamo (all MCZ). Jamaica: Montego (USNM); St. Anne's (MCZ); Spanish Point, Pembroke Parish; Great Pedro Bay; Caymanas; Carlisle Bay, in 6 fathoms (all USNM).

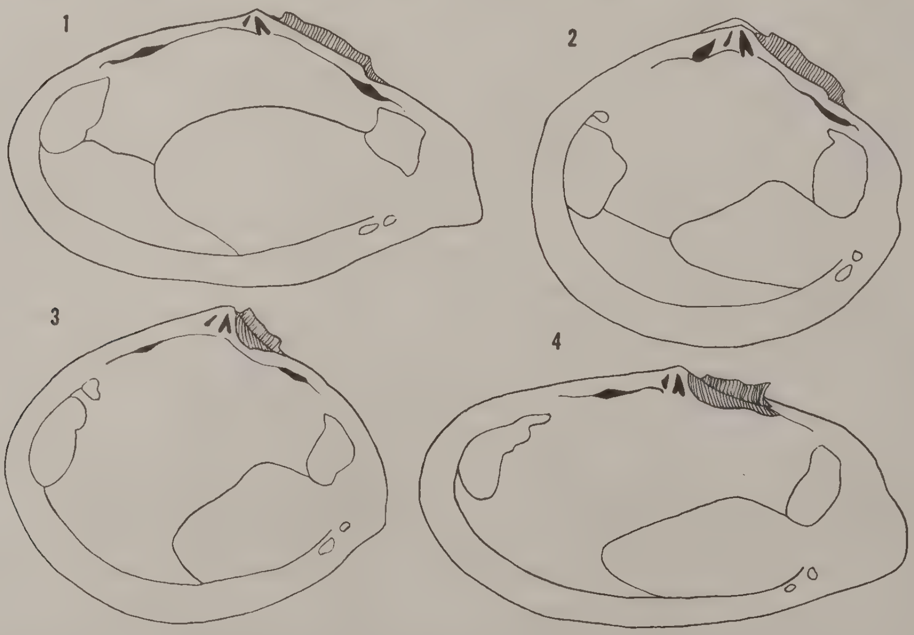

Plate 134. Figs. 1–4. Diagrammatic illustration of the internal surface of the right valve showing the dental configuration and muscle scars. Fig. 1. *Tellina listeri* Röding (about 1.2x) [L=60 mm.]. Fig. 2. *Tellina fausta* Pulteney (about 1.2x) [L=66 mm.]. Fig. 3. *Tellina laevigata* Linnaeus (about 1.3x) [L=45 mm.]. Fig. 4. *Tellina magna* Spengler (about 1.2x) [L=60 mm.].

(all MCZ). Virgin Islands: Anegada Island, in 4–20 feet (ANSP); Virgin Gorda; Marine Cay, Tortola; White Bay and Monkey Point, Guana; St. Thomas; Altona, Lagoon, St. Croix (all MCZ). Lesser Antilles: St. Kitts (MCZ); St. Lucia, in 10 Hispaniola. Haiti: Baie des Flamands; Jérémie (both USNM); Miragoane (MCZ); Santo Domingo: Siete Hermanos (USNM); Puerto Sosua; Monte Cristi; Puerto Plata fathoms; St. Vincent; Guadeloupe; Barbados (all USNM); Carriacon Island, Grenadines; Pigeon Point, Tobago (both MCZ). Caribbean Islands: Georgetown Harbor, Frank Sound Reef and Palmetto Point, Grand Cayman (all ANSP); Swan Island (MCZ). Colombia: Covenas, off Bolivar; Cartagena; Santa Marta (all USNM). Venezuela: El Roque Island; Aruba Beach (both USNM). Brasil: 150 miles NE of Bahia (MCZ).

Subgenus **Laciolina** *Iredale*

Scrobiculina Dall 1900, Proc. U.S. Nat. Mus., **23**: 290 (type species, *Scrobicularia viridotincta* 'Carpenter' Dall, *non* Carpenter 1864, original designation).[1]

Laciolina Iredale 1937, Australian Zoologist, **8**(4): 241 (type species, *Tellina quoyi* Sowerby 1868, original designation).

Description. Shell medium to large in size, ovate to elliptical in shape, subsolid to solid, left valve somewhat inflated and with a flexure to the right posteriorly. Sculpture more or less smooth. Ligament of variable strength but with a strong thickened calcareous element subtended by a flattened nymphal callosity. Lateral teeth variously developed. In the right valve, both a subproximal anterior and a distal posterior lateral tooth present. In the left valve, the subproximal anterior lateral tooth developed; posterior lateral tooth developed or obsolete; rarely both laterals weak. Pallial sinus linguiform, pointed or rounded anteriorly and well separated from the anterior adductor muscle scar. Confluence of the pallial sinus with the pallial line limited to the posterior quarter of the valve.

The members of *Laciolina* tend to be rather large shelled and are therefore conspicuous. By and large, their simplest characterization rests in the structure of the ligament which possesses a typically thickened calcareous element. This internal portion of the ligament is greater in dorso-ventral proportion nearer the umbo and tapers posteriorly to the end of the nymph (see Plate 134, figs. 3–4). *Laciolina* has representatives in the tropical seas of the world, but it has not been discovered in the fossil record in the Western Atlantic.

KEY TO THE SPECIES OF *LACIOLINA* IN THE WESTERN ATLANTIC

1. Shell suborbicular; right posterior lateral dentition developed . . . . . . *laevigata*
   Shell elongate-elliptical; right posterior lateral dentition obsolete . . . . *magna*

Tellina (Laciolina) laevigata *Linnaeus*

Plate 133, fig. 6; Plate 134, fig. 3

Tellina laevigata Linnaeus 1758, Systema Naturae, Ed. 10, p. 675 (In O Europaeo et Indico) [type locality, here restricted, Harrington Sound, Bermuda; type specimens, Collection of Linnean Society, London].

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[1] *Scrobularia viridotincta* Carpenter is macomoid in its morphological features. Dall's *Scrobiculina* has been given the rank of a junior synonym of *Psammotreta* (See Boss. 1964. The Veliger, **6**(4): 208–210).

Tellina concinna Philippi 1844, Abbildungen und Beschreibungen Conchylien, **1:** p. 11, *Tellina*, pl. 2, fig. 1 (no locality) [type locality, here restricted, Harrington Sound, Bermuda; types not seen], *non concinna* Edwards 1847.

Tellina laevis 'Chemnitz' Krebs 1864, The West Indian Marine Shells, p. 102.

Tellina bayleana Bertin 1876, Nouv. Arch. Mus., Paris, 2 ser., **1:** 256, pl. 8, figs. 3a–b (Guadeloupe) [type specimens, L'Ecole des Mines, Paris].

Tellina (*Tellina*) *laevigata* Linnaeus. Dall 1900, Proc. U.S. Nat. Mus., **23:** 293.

Tellina laevigata stella Davis 1904, Nautilus, **17**(11): 128, pl. 4, fig. 2 (Flatt's Inlet, Bermuda) [syntypes, ANSP, nos. 86921 and 109554].

Description. Shell reaching 94 mm. (about 3¾ inches) in length and 78 mm. (about 3 inches) in height, suborbicular, with a rather sharp posterior flexure to the right posteriorly. Valves thin, nearly fragile in young specimens. Umbos subcentral, elevated and pointed. Anterior margin broadly rounded; ventral margin with a postbasal arcuation; anterior dorsal margin gently sloping; posterior dorsal margin descending steeply; posterior margin nearly straight and forming a characteristic truncation. Sculpture consisting of regular concentric lines of growth which become heavy and coarse peripherally; radial lirations often present. Ligament dark brown to black and sunken. Calcareous portion of the ligament rather thick and supported by a nymphal callosity. In the left valve, the cardinal complex consists of an anterior elongate strong bifid tooth with the anterior lobe being much the larger, and of a posterior elongate laminate tooth; anterior lateral tooth weak and closer to the cardinal complex than the posterior tooth which is distal and well developed. In the right valve, the cardinal complex consists of a posterior thin bifid tooth with subequal lobes and of an anterior weak laminate tooth; the posterior lateral tooth is weaker and further removed from the cardinal complex than the strong, somewhat proximal anterior lateral tooth. Adductor muscle scars well impressed. Anterior and posterior adductor scars subequal and of a similar shape. Pallial sinus short, widely separated from the anterior adductor scar, rising only slightly and descending gently to a point more or less beneath the anterior lateral tooth where it falls abruptly to the pallial line; confluence short. Externally the shell is predominantly white in color but traces of yellow, fleshy-pink, orange and red are often evident either in a suffused or radial pattern.

length	height	width	
94 mm.	78 mm.	—	Bermuda
72	55	19 mm.	Lake Worth, Florida
57	40	14	Grand Bahama, Bahama Islands
57	45	16	Harrington Sound, Bermuda
43	34	12	St. Croix, Virgin Islands

Remarks. Among the characters of this species, none is as variable as the color and the pattern of color exhibited externally. The synonyms of *laevigata* have all been established on the basis of color. Some individuals are pure white, cream-yellow, or suffused with orange; others possess a peripheral band of similar colors while still others are variously rayed with orange, pink or red.

Tellina magna Spengler has been placed with *T. laevigata* in *Laciolina* because of the great similarity in the shape of the pallial sinus, the formation of the hinge and ligamental mechanisms and the disposition of the right anterior lateral tooth. From *magna*, *laevigata* is immediately separated by its orbicular shape, the radial dispensation of its coloration and the presence of a developed right posterior lateral tooth.

In the Eastern Pacific, *Tellina ochracea* Carpenter [=*viridotincta* of authors] is the nearest relative to *laevigata;* it is immediately separated by its distinctly thinner shell, and different coloration and proportions. *Tellina chloroleuca* Lamarck from the Philippines is closely related but is differentiated by its thinner shell, more elongate form, red umbos and somewhat sharper posterior flexure.

The fossil record of *Tellina laevigata* is not documented. In habit, it prefers relatively shallow water from depths of two feet to six fathoms; the usual substrate seems to be sand.

Range. This species has been found as far north as Beaufort Harbor, North Carolina. It occurs in Bermuda, throughout the Bahama Islands, and on the west coast of Florida as far north as Tampa Bay; it ranges southward through the Antilles to Venezuela.

Specimens examined. North Carolina: Beaufort Harbor (ANSP); *Albatross I* station 2597, 20 miles ESE of Cape Hatteras (34°57′ N; 75°43′ W), in 15 fathoms (USNM). Florida: Lake Worth; Bird Key, Biscayne Bay; Hawk Channel; Caesar's Creek Bank; Turtle Harbor (all USNM); Key West (MCZ); Charlotte Harbor; Tampa Bay (both USNM). Bermuda: St. George; Castle Harbour; Trunk Island; Long Bay, Warwick (all MCZ). Bahama Islands: Grand Bahama; Long Island; Turks Island (all MCZ). Cuba: Cape Cajon; Santa Rosa; Esperanza; Havana (all USNM); Matanzas; Cayo Frances, Caibarien; Punta Alegre, Camagüey (all MCZ). Virgin Islands: Anegada; St. Thomas; St. Croix (all ANSP). Lesser Antilles: Barbados; Tobago (both MCZ). Caribbean Islands: Grand Cayman (ANSP). Venezuela: La Guaira (USNM); *Atlantis* Cruise 240, 30 miles N of Cabo Cadera, in 150 fathoms (MCZ).

Tellina (Laciolina) magna *Spengler*

Plate 133, figs. 4–5; Plate 134, fig. 4

Tellina magna Spengler 1798, Skrivter Naturhistorie-Selskabet, **4**(2): 76, p. 12, fig. 1 (Fra de Middelhavet) [type locality, here corrected and restricted, St. Croix, Virgin Islands; lectotype, here selected, Zoological Museum, Copenhagen].

Tellina acuta Wood 1815, General Conchology, p. 157, pl. 44, fig. 1 (West Indies) [type locality, here restricted, St. Croix, Virgin Islands; types not seen].

Tellina elliptica Lamarck 1818, Animaux s. Vertèbres, **5**: 524 (provenance inconnue), [type locality, here restricted, St. Croix, Virgin Islands; holotype, Museum d'Histoire Naturelle, Paris], *non* Brocchi 1814, *nec* Sowerby 1867.

Tellina vitrea d'Orbigny 1842 [in] Sagra, Hist. L'Ile Cuba, Atlas, pl. 26, figs. 4–5; 1845, Spanish Text, **2**(5): 304 (Guadeloupe); 1853, French Text, Mollusques, **2**: 253 [holotype, BMNH, no. 54.10.4.510].

Tellina sol Hanley 1844, Proc. Zool. Soc. London, p. 142 (locality unknown) [type locality, here restricted, St. Croix, Virgin Islands; holotype, BMNH].

Phylloda sol Hanley. Bertin 1878. Nouvelles Arch. Mus., Paris, 2 ser., **1**: 329.

Tellina (*Angulus*) *magna* Spengler. Dall 1900, Proc. U.S. Nat. Mus., **23**: 295.

Tellina (*Scrobiculina*) *magna* Spengler, Warmke and Abbott 1961, Caribbean Sea Shells, p. 194.

Description. Shell extending to 122 mm. (about 4¾ inches) in length and to 65 mm. (about 2½ inches) in height, laterally compressed, not tumid and valves uniformly thin. Umbos just posterior to the middle and not inflated. Anterior margin smoothly rounded; ventral margin arcuate; anterior and posterior dorsal margins gently sloping. Shell sculptured with regularly and closely spaced concentric lines of growth which are stronger on the left valve and with extremely fine radial lirations which are most evident on the anterior slope. Ligament light brown in color with an exceptionally thick calcareous portion which is sunken. In the left valve, the cardinal complex consists of an anterior strong deltoid bifid tooth with subequal lobes and of a thin posterior laminate tooth; lateral teeth totally absent or obsolete; rarely there is a weak proximal anterior tubercle. In the right valve, the cardinal complex consists of an elongate posterior bifid tooth with subequal lobes and a variously developed anterior laminate tooth; anterior lateral tooth well developed, small and proximal; posterior lateral absent or represented by an obsolete distal tubercle. Adductor muscle scars fairly well impressed. The posterior adductor muscle scar long, narrow and crescent shaped; the anterior adductor scar irregular. Pallial sinus short, shallow and constricted; its dorsal margin extends little above the ventral borders of the adductor scars; it is far removed posteriorly from the anterior adductor and confluent with the pallial line for about one third of its length. The pallial line swings sharply upward posteriorly and its terminus is far removed from the posterior margin of the shell. Externally the color may be white or fleshy-pink; often concentric alterations of color are evident as well as yellowish or pinkish rays emanating from the umbos. The right valve tends to be more strongly colored. The umbos are generally a rich golden yellow, often tending toward red. Internally the shell is mostly white with some suffusion of yellow radiating from the umbo.

length	height	width	
91.0 mm.	51.9 mm.	17.0 mm.	Lectotype of *magna* Spengler
20.5	11.0	3.6	Holotype of *vitrea* d'Orb.
96.0	58.8	17.2	Holotype of *sol* Hanley
122.0	65.0	22.0	Pass-a-grille, Florida
82.0	48.0	13.0	Trinity Bay, Martinique
22.0	10.5	3.5	Great Inagua, Bahamas

Remarks. This is one of the largest if not the largest of Western Atlantic tellins. Among the variable characters possessed by the species, the color and its pattern of distribution seems to be the greatest. Generally the shell is white with umbonal concentrations of yellow, fleshy-pink, orange or red; however, these colors in some individuals permeate the whole shell while in others they are disposed in a radial pattern emanating from the umbo. The hinge of *magna* is deeply inset and its calcareous portion very well developed. In respect to this character, *magna* may be compared with *laevigata*, *ochracea* of the Eastern Pacific and even *chloroleuca* of the Indo-Pacific, but its total lack of true lateral hinge dentition save for the right anterior lateral tooth precludes a too closely assigned relationship with *laevigata*. Dall (1900a) included this species in his diagnosis of *Angulus* and went on to say that though the species attained a large size, it agreed with the characteristics of *Angulus;* however, the strong, inset ligament and the subproximal, but quite well removed, right anterior lateral are unlike other species of *Angulus* and the nature of these characters alone places this species with *Laciolina*.

Ardeamya columbiensis (Hanley) of the Eastern Pacific is very close to *Tellina magna* in all its characteristics except in the complete lack of lateral dentition. It is probable that the great similarity in shape as well as the similarity of the configuration of the pallial sinus and of the ligamental structure are convergent. *Tellina magna* lacks the greenish-gray periostracum of *Ardeamya*.

Range. In the north, this species is found in Bermuda throughout the Bahamas, on the east coast of Florida as far north as Lake Worth and on the west coast of Florida as far north as Fort Walton. It ranges south through the Antilles to Martinique.

Specimens examined. FLORIDA: Peanut Island, Lake Worth; Grassy Key (both ANSP); Big Pine Key; Western Dry Rocks; Tortugas; Captiva; Long Key; Anne Marie Key; Pass-a-grille Beach (all MCZ); Anclote Keys; Cedar Keys (both USNM); Fort Walton (ANSP). BERMUDA: Castle Harbor; Trunk Island (both MCZ). BAHAMA ISLANDS: Grand Bahama; South Bimini Island; New Providence; Long Island; Great Inagua Island (all MCZ). CUBA: Habana; Cardenas (CNM); Punta Alegre, Camagüey (MCZ). VIRGIN ISLANDS: St. John (IMBPR); St. Croix (ANSP). LESSER ANTILLES: Trinity Bay, Martinique (BMNH). CARIBBEAN ISLANDS: Georgetown, Grand Cayman (ANSP).

Subgenus **Arcopagia** *Brown*

Arcopagia Brown 1827, Illustrations Conch. Great Britain and Ireland, pl. 16, fig. 8 (type species, *Tellina crassa* Pennant 1776, subsequent designation, Hermannson 1846, p. 76).

Cydippe Leach 1852, Synopsis Moll. Great Britain, p. 314 (type species, *Cydippe listeriana* Leach [= *Tellina crassa* Pennant], monotype), *non* Escholtz 1821.

Description. Shell medium to large in size, ovate, solid, equivalve and more or less equilateral. Lateral dentition well developed. In the right valve, both lateral teeth distinct and strong; posterior lateral tooth distal to cardinal complex and anterior lateral tooth subproximal or distal to the cardinal complex. Pallial sinus of various configurations. In the type, it rises obliquely and descends to the terminus of the pallial line so that no confluence occurs; however, the pallial sinus may be confluent with the pallial line for nearly all its length. Sometimes a linear scar connects the anterior adductor muscle scar and the pallial sinus.

Arcopagia in its broad sense is herein treated as a subgenus whereas some authors have used it as a full genus and many workers have divided it into numerous sections. Some traits which typify the group are unstable and liable to alteration among related species; however, the orbicular shape and general thickness of the valves typify the group. The lateral dentition is stronger in the right valve than in the left, and the position of these teeth is variable although the posterior lateral tooth is nearly always distally removed from the cardinal complex. The left lateral dentition is characterized by the obsolescence of the distal posterior tooth and by a variable placement of the anterior tooth.

The subgenus may be traced back to the Cretaceous (Stoliczka, 1870). Numerous species have been described in Cenozoic deposits. For example, the group is well represented in the Eocene of the Paris Basin. In the Recent fauna, the group appears to be most highly concentrated in the Indo-Pacific. Most species seem to prefer a tropical habitat, but there are some exceptions, for some species are temperate or even boreal in their distribution.

Tellina (Arcopagia) fausta *Pulteney*

Plate 134, fig. 2; Plate 135, figs. 1–2

Tellina remies 'Linnaeus' Born 1870, Museum Caesarum Vindobonensis, p. 36, pl. 2, fig. 11.

Tellina fausta Pulteney 1799, Catalogues of Dorsetshire, p. 92; 1813, 2 ed., p. 30, pl. 5, fig. 5 (British shore, Dorsetshire) [type locality, here corrected and restricted, Kingston, Jamaica; types lost].

Tellina laevis Wood 1815, General Conchology, p. 181, pl. 37, fig. 1 (West Indies) [type locality, here restricted, Kingston, Jamaica; types not seen].

Tellina (Arcopagia) fausta Donovan. H. and A. Adams 1856, Genera Recent Mollusca, **2**: 396.

Tellina elliptica Sowerby 1868, Conch., Icon., **17**, **Tellina**, pl. 43, fig. 251 (locality unknown), [type locality, here restricted, Kingston, Jamaica; holotype, BMNH, no. 1900.3.19.6], *non* Sowerby 1867, *nec* Brown 1814, *nec* Lamarck 1818, *nec* Brown 1827.

Tellina ellipsis Sowerby 1869, Ibid., Index.

Cyclotellina (*Cyclotellina*) *fausta* Pulteney. Thiele 1935, Handbuch Weichtierkunde, **2**: 915.

Arcopagia fausta Pulteney, Warmke and Abbott 1961, Caribbean Seashells, p. 197, pl. 4, fig. 1.

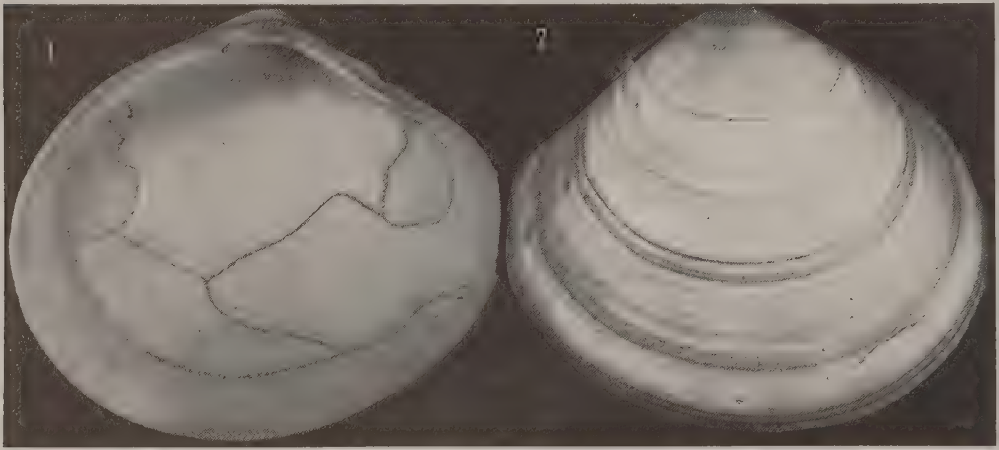

Plate 135. *Tellina fausta* Pulteney. Fig. 1. Internal view of the right valve, Biscayne Bay, Florida, MCZ 209049 (about 1.2x) [L=59 mm.]. Fig. 2. External view of the right valve, Tobago, West Indies, MCZ 143625 (about 1.1x) [L=64 mm.].

Description. Shell reaching 98 mm. (about 4 inches) in length and 90 mm. (about 3½ inches) in height, suborbicular, solid and rather tumid. Umbos subcentral and somewhat inconspicuous. Anterior and ventral margins broadly rounded; anterior dorsal margin very gently sloping; posterior dorsal margin somewhat steep; posterior margin straight and forming a characteristic truncation. Sculpture consisting of somewhat irregularly spaced growth bands which have a tendency to become stronger on the anterior and posterior slope; an extremely fine, microscopic pattern of radial striae is evident. In the left valve, the cardinal complex consists of an anterior strong, slightly skewed bifid tooth and of a posterior thin, elongate laminate tooth; the anterior lateral tooth strong and proximal to the cardinal complex; the posterior lateral tooth distal and smaller than the anterior tooth. In the right valve, the cardinal complex consists of a posterior, skewed, strong bifid tooth and of an anterior elongate laminate tooth; the anterior lateral tooth proximally adjacent to the cardinal complex, protuberant and well developed. A strong internal rib extends radially from the umbo to the anterior adductor muscle scar. Ligament black or dark brown and protuberant. Calcareous element of the ligament subtended by a nymphal callosity. Adductor muscle scars well impressed. Anterior adductor scar large; posterior adductor scar irregularly oval. Pallial sinus not equal in opposite valves; pallial sinus in the left valve longer and closer to the anterior adductor scar than that of the right valve. The sinus rises sharply posteriorly but only for a short distance, then it descends gently anteriorly and falls to the pallial line far posteriorly; confluence short. Externally, the shell is usually a dull white. Internally polished and with traces of a pale yellow suffusion.

length	height	width	
26 mm.	20.8 mm.	9.5 mm.	Holotype of *elliptica* Sow.
98	90.0	40.0	New Providence, Bahamas
69	63.0	28.0	Punta Jorobado, Puerto Rico
30	26.0	12.0	Guantanamo, Cuba
17	8.0	6.0	Jamaica

Remarks. Tellina fausta is one of the largest of all Western Atlantic tellinids; it possesses the thickest, strongest and heaviest shell of all the species in that area and is quite distinguishable from all others on that basis alone. Its immediate ally and its closest relative, *Tellina remies* Linnaeus, occurs in the Indo-Pacific region. In *fausta*, the shell is more or less smooth whereas in *remies*, heavy, rounded, raised concentric sculpture is typical.

Dall (1900b, p. 1031) has documented the occurrence of *Tellina fausta* in the Pliocene marl of Caloosahatchie, Florida. He also listed a number of Eocene species from the Clairbornian formation which may have some relationship with the ancestry of *fausta*.

In young individuals of *Tellina fausta*, the interior of the shell is often brightly colored with yellow and this coloration may show through externally. In adults, most of this external coloration is lost. There is present a brownish periostracum on living individuals.

Robertson (1961) has noted that *Tellina fausta* at Bimini lives in a coarse sand substrate at a depth of one foot, mostly among *Thalassia* rhizomes. Abbott (1958, p. 135) reported the occurrence of this species at Grand Cayman in water 4–6 feet deep over clear sand. The maximum depth record is 15 fathoms.

Range. This species is distributed from off the east coast of Florida near Lake Worth through the Florida Keys and the Bahamas, south to Tobago and the north coast of South America.

Specimens examined. NORTH CAROLINA: Cape Lookout (USNM). FLORIDA: Lake Worth (MCZ); Hillsboro Inlet (ANSP); Key Biscayne (CNM); Elliot's Key (MCZ); Rodriguez Island and Garden Cove, Key Largo (both ANSP); Grassy Key; Key Vaca; Bonefish Key; Boca Chica Key (all MCZ); Key West; Tortugas (both USNM). MEXICO: Veracruz; Isla del Carmen, Campeche (both MCZ). BRITISH HONDURAS: Belize (USNM; MCZ). HONDURAS: (BMNH). NICARAGUA: (ANSP). COSTA RICA: (ANSP). PANAMA: Mt. Hope (subfossil, ANSP); Brujas Point (MCZ); Cristobal; Colon; Fox River (all USNM). BERMUDA: Castle Harbor (subfossil, MCZ). BAHAMA ISLANDS: West End Point, Hawk's Bill Creek and Holmes Cay, Grand Bahama; Alicetown, North Bimini; Dick's Point, Nassau, New Providence; Eleuthera (all MCZ); Lisbon Creek Reef, Andros (USNM); Orange Creek and Little San Salvador, Cat Island (MCZ); Cockburn Town, Watlings Island; Exuma (both USNM); Long Island; Matthew Town, Great Inagua (both MCZ); Turks Island (USNM). CUBA: *Barrera* station 218, Cayo Hutia Reef; *Barrera* station 20, Santa Lucia, in 2–4 fathoms (both USNM); Jaimanitas, Habana (MCZ); Cayo Galendo, Cardenas Bay (ANSP); Cabanas Bay (USNM); Cayo Francés, Caibarien; Santa Maria Key, off Punta Alegre, Camagüey; Rancho Aluna, Cienfuegos Bay; Castillo de Jagua, Cienfuegos; mouth of Yateras River, Oriente; Guantánamo (all MCZ). JAMAICA: Green Island Harbour; Abingdon (both USNM); Montego (MCZ); Runaway Bay (USNM); Whitehouse Bay (MCZ); Ocho Rios; Port Maria; Jack's Bay; Robin's Bay; Harboreale, Annotta Bay; Port Antonio; Black River; Great Pedro Bay; Kingston; Buff Bay (all USNM); Pedro

Bank (MCZ); Port Royal; Palisadoes (both USNM). HISPANIOLA. HAITI: Cape Haitien (MCZ); Carpentier; Port au Prince (both USNM); Miragoane (MCZ); Jerémié; Baie Anglaise; Coteaux; Les Cayes (all USNM); Aquin (MCZ); Bizoton; Petit Groove; Saltrou (all USNM). SANTO DOMINGO: Siete Hermanos (USNM); Monte Cristi; Puerto Plata; Santa Bárbara de Samaná; Santo Domingo (all MCZ). PUERTO RICO: Mayaguez (MCZ); Porto Real (USNM); Cabo Rojo Light House (IMBPR); Ponce; Punta Jorobado; San Juan (all MCZ); Culebra Island (USNM); La Parquera (MCZ). VIRGIN ISLANDS: Loblolly Bay, Anegada (ANSP); Tortola (USNM); Monkey Point, Guana Island; Norman Island; St. Croix; St. Thomas (all MCZ). LESSER ANTILLES: Anguilla Island (BMNH); St. Martins (ANSP); Orange Bay, St. Eustatius Island (MCZ); St. Kitts (ANSP); Nevis Island (MCZ); Mill Reef Club, St. Philip, Antigua (MCZ); Falmouth Harbour, Antigua, in 3-6 fathoms (USNM); Guadeloupe; Martinique (BMNH); Villa, St. Vincent (USNM); Port Castries, St. Lucia (MCZ; USNM); Bathsheba and St. Lawrence, Barbados (both USNM); Maxwell's Coast, Barbados (MCZ); Grande Anse, Grenada (MCZ); Union, Admiralty Bay, Bequia Island and Carriacou Island, The Grenadines (both MCZ); Pigeon Point, Tobago (MCZ). CARIBBEAN ISLANDS: Gun Bay, Grand Cayman Island (ANSP); Swan Islands (USNM; MCZ); Aruba (USNM). COLOMBIA: Cartagena Bay (USNM; MCZ); Puerto Colombia (USNM). VENEZUELA: La Guaira (USNM).

Subgenus **Phyllodina** *Dall*

Phyllodina Dall 1900, Proc. U.S. Nat. Mus., **23:** 290 (type species, *Tellina squamifera* Deshayes 1855, original designation).

Description. Shell of small and medium size, elongate-elliptical, mostly equilateral and equivalve. Umbo pointed, central to subcentral. Sculpture primarily concentric and sometimes differentiated posteriorly in the weakly flexed rostral area. Ligament short and somewhat sunken. Lateral dentition of right valve consisting of developed anterior and posterior lateral teeth distally placed in relation to the cardinal complex. Pallial sinus rising obliquely and falling obliquely to the pallial line; confluence short, limited to the posterior quarter of the ventral length of the pallial line. The pallial sinus is connected to the anterior adductor muscle scar by a linear scar.

The taxon *Phyllodina* of Dall forms a more or less natural group characterized by an obliquely rising, dorsally flattened, narrow and short pallial sinus which is connected with the anterior adductor scar by means of a single linear scar. The particular shape of the shell, being more or less elongate but not ovate, and the distinctive concentric sculpture circumscribe the whole group.

Phyllodina has representatives in the Miocene of North America and possessed a more northerly distribution during the Tertiary. It is represented by two species in the Eastern Pacific and two in the Western Atlantic, and there also are some Indo-Pacific representatives.

KEY TO SPECIES OF *PHYLLODINA* IN THE WESTERN ATLANTIC

1. Shell with spinose sculptural foliation along the posterior slope . . . *squamifera*

Shell without spinosities posteriorly . . . . *persica*

Tellina (Phyllodina) squamifera *Deshayes*
Plate 136, fig. 1; Plate 137, fig. 1; Plate 140, fig. 3

Tellina squamifera Deshayes 1855. Proc. Zool. Soc. London, **22:** 365 (Chinese Seas) [type locality, here corrected and restricted, off Miami Beach, Florida; holotype, BMNH].

Tellina (*Arcopagia; Phyllodina*) *squamifera* Deshayes. Dall 1900, Proc. U.S. Nat. Mus., **23:** 290.

Phylloda (*Phyllodina*) *squamifera* Deshayes. Thiele 1935, Handbuch Weichtierkunde, **2:** 918.

Phyllodina squamifera Deshayes. Olsson 1961, Panamic-Pacific Pelecypoda, p. 397.

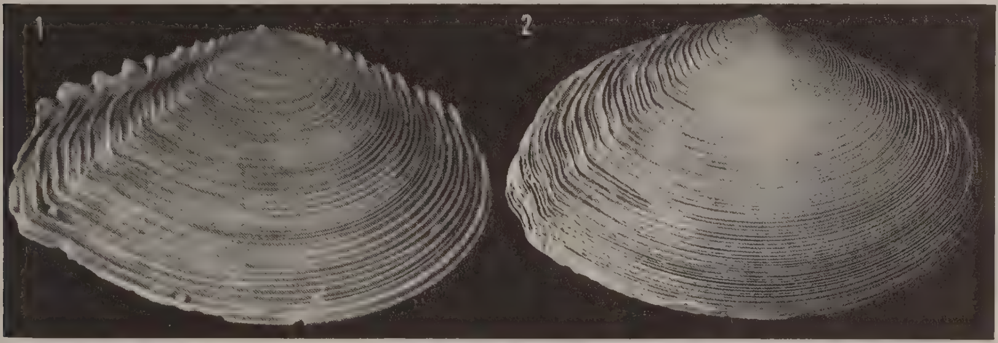

Plate 136. Fig. 1. *Tellina squamifera* Deshayes, external view of the right valve, off Sombrero Key, Florida MCZ 168730 (about 5x) [L=15.5 mm.]. Fig. 2. *Tellina persica* Dall and Simpson, external view of the right valve, Tobago, West Indies, MCZ 243066 (about 4.5x) [L=21.5 mm.].

Description. Shell extending to 26.8 mm. (about 1 inch) in length and to 16.4 mm. (about $\frac{1}{2}$ inch) in height, elongate, somewhat compressed with the left valve markedly more convex and with a strong flexure to the right posteriorly. Umbos small and pointed. Anterior margin smoothly and somewhat narrowly rounded; ventral margin convex, rising slightly posteriorly; anterior and posterior dorsal margins straight, subequal and gently sloping; posterior margin more or less straight, and forming an oblique truncation. Sculpture consisting of rather evenly spaced, slightly raised ribs separated by broad depressed bands; radial sculpture lacking. Strong posterior ridge developed in the right valve; concentric sculpture strongest on the posterior slope. The raised concentric ribs extend beyond the dorsal margin of the valve to form trigonal foliations which give the shell a serrate appearance. Ligament light to dark brown, short and protuberant. Calcareous element of the ligament subtended by a narrow, weak nymphal callosity. In the left valve, the cardinal complex consists of an anterior, elongate bifid tooth whose posterior lobe is the larger and of a posterior thin laminate tooth with a broadened base; anterior lateral tooth distal, weak and poorly developed; no true posterior lateral. In the right valve, the cardinal complex consists of a posterior strong subdeltoid bifid tooth with subequal lobes and of an anterior, thin, laminate tooth; anterior lateral distal, strong and well developed; posterior lateral distal, strong and well developed; the laterals are very long with grooves above. Adductor muscle scars poorly impressed. Pallial sinus rising obliquely, more or less flattened above and obliquely descending to the pallial line and uniting far posteriorly; it is connected to the anterior adductor scar by a short linear scar; confluence short. Externally the shell is white; internally, white suffused with yellow in the umbonal region and sometimes red or yellow on the posterior slope.

length	height	width	
20.8 mm.	12.0 mm.	4.7 mm.	Holotype of *squamifera* Deshayes
26.8	16.4	—	off Fowey Light, Florida
19.2	11.9	3.9	off Sombrero Key, Florida
11.7	6.9	2.3	off Miami, Florida
5.7	3.7	—	off Fowey Light, Florida

Remarks. This species may be at once separated from the nearest living ally in the Western Atlantic, *Tellina persica* Dall and Simpson, by its strong posterior dorsal foliations and its more coarse and raised concentric sculpture. In the Eastern Pacific, *squamifera* is most closely related to *T. pristiphora* Dall which is shorter and higher in the proportions of the shell. In addition, Dall has indicated that *pristiphora* is greenish whereas *squamifera* is usually white with suffusions of yellow and some red along the posterior slope. *Tellina leptalea* Gardner from the Shell Bluff, Shoal River formation of Florida is a Middle Miocene ancestor of *T. squamifera* and *T. dodona* Dall from the Miocene Oak Grove formation of Florida appears to be related to the lineage of both *T. squamifera* and *T. pristiphora.*

There is some variation in the thickness of the valves, especially in older individuals where the shell becomes quite solid. In some cases, the shell is less elongate than normal and it may become even somewhat subtrigonal. In immature stages, the shell has a slightly different form. The posterior truncation is broader, the shell tends to be vitreous, almost transparent, extremely fragile and thin, and the concentric growth lines are fewer, being wider and more undulate in immature specimens.

According to Parker (1960, p. 335), *Tellina squamifera* is a member of the 12–14 fathoms assemblage on sandy bottoms in the northern Gulf of Mexico,

Range. This species possesses a range which extends as far north as Cape Hatteras, North Carolina and south throughout the Florida Keys and Reefs, into the Gulf of Mexico and as far west as Texas and Mexico.

Specimens examined. NORTH CAROLINA: *Albatross I* station 2595, 22 miles ESE of Cape Hatteras (35°08′ N; 75°05′ W), in 63 fathoms (USNM). FLORIDA: off Palm Beach, in 50–100 fathoms (ANSP); off Miami, in 10–60 fathoms; off Fowey Light, in 25–125 fathoms; off Ragged Key; off Triumph Reef; off Ajax Reef; off Turtle Harbor (all USNM); off Sombrero Key, in 20–66 fathoms; off Looe Key, in 25–30 fathoms; off American Shoals, in 25–30 fathoms (all MCZ); off Sambo Reef; off Key West (both USNM); off Pelican Shoals, in 45 fathoms (MCZ); *Albatross I* station 2410, 80 miles N of Dry Tortugas (26°47′ N; 83°25′ W), in 28 fathoms; *Albatross I* station 2404, 35 miles S of Cape San Blas (28°44′ N; 85°16′ W), in 60 fathoms (both USNM). ALABAMA: *Albatross I* station 2367, 60 miles S of Mobile Bay 29°24′ N; 88°04′ W), in 32 fathoms (USNM). TEXAS: off Port Isabel, in 50 fathoms; 80–100 miles S of Port Isabel, in 40 fathoms (both MCZ).

Tellina (Phyllodina) persica *Dall and Simpson*

Plate 136, fig. 2; Plate 137, fig. 2

Tellina (*Arcopagia; Phyllodina*) *persica* Dall and Simpson 1901, Bull. U.S. Fish. Comm., **20**(1): 479, pl. 55, fig. 1 (Mayaguez Harbor, in 20–30 fathoms) [holotype, USNM, no. 159991].

Tellina (*Arcopagia*) *persica* Dall and Simpson. McLean 1951, N.Y. Acad. Sci., **17**(1): 94.

Tellina (Eurytellina) persica Dall and Simpson. Warmke and Abbott 1961, Caribbean Seashells, p. 195, pl. 29, fig. g.

Description. Shell extending to 25 mm. (about 1 inch) in length and to 13 mm. (about ½ inch) in height, subquadrate, slightly inflated with the left valve slightly more convex and with a short but distinct posterior flexure to the right. Umbos central, small and markedly pointed. Anterior margin smoothly, but very narrowly rounded; ventral margin slightly convex and rising gently posteriorly; anterior dorsal margin gently sloping and straight; posterior dorsal margin somewhat convex, very gently sloping and short; posterior margin biangulate, with both portions straight and forming a rather blunt truncation. Sculpture consisting of raised concentric ribs rather evenly spaced and separated by narrow bands except on the posterior half of the right valve where the ribs become fewer, much stronger, lamellate and separated by wider bands. Radial sculpture consisting of exceedingly weak and faint lirations which are totally absent on the posterior half of the right valve. Ligament brown, strong and somewhat sunken. Calcareous portion of the ligament not strongly developed and subtended by weak nymphal callosities. In the left valve, the cardinal complex consists of an anterior strong deltoid bifid tooth whose posterior lobe is the stronger and of a posterior extremely well developed, elongate, subdeltoid laminate tooth; anterior lateral tooth distal, rather weak, but stronger than the distal obsolete posterior lateral. In the right valve, the cardinal complex consists of a posterior, skewed, strong, bifid tooth with subequal lobes and a well developed, short, anterior laminate tooth which is much weaker than the same in the opposite valve; anterior lateral tooth strong and distal; posterior lateral tooth stronger and distal. Adductor muscle scars rather poorly impressed. Anterior adductor muscle scar longer and narrower than the posterior. Pallial sinus rising abruptly and obliquely, flattened above, falling obliquely to and uniting with the pallial line far behind the anterior adductor scar; confluence short. A faint linear scar sometimes unites the anterior adductor scar with the pallial sinus. Externally and internally, the shell is white suffused with apricot, concentrated in the umbonal region and on the disc.

length	height	width	
20.6 mm.	12.7 mm.	5.8 mm.	Holotype of *persica* Dall and Simpson
24.2	13.2	5.8	Mayaguez, Puerto Rico
16.2	10.1	4.0	" " "
14.5	9.2	3.8	" " "
7.0	4.0	—	off Scarborough, Tobago

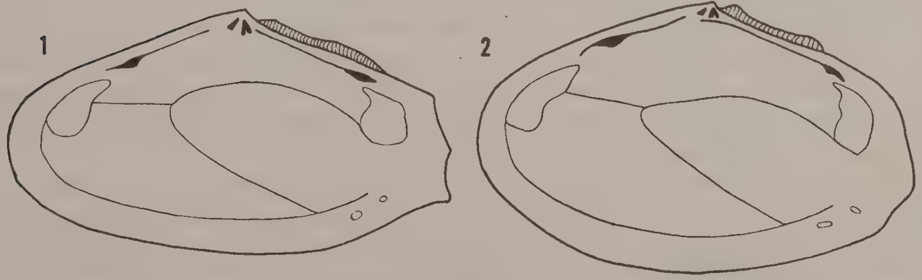

Plate 137. Figs. 1–2. Diagrammatic illustration of the internal surface of the right valve showing the dental configuration and muscle scars. Fig. 1. *Tellina squamifera* Deshayes (about 4.4x) [L=20 mm.]. Fig. 2. *Tellina persica* Dall and Simpson (about 4.2x) [L=21 mm.].

Remarks. By the paucity of material in various collections, *Tellina persica* may be judged to be a relatively rare species with a restricted distribution. In the Atlantic fauna, it is most closely related to *T. squamifera* Deshayes from which it may be immediately distinguished by its lack of posterior dorsal foliations, its subquadrate shape, and its smooth and regular concentric sculpture. It is also quite similar to the Eastern Pacific species, *T. fluctigera* Dall from which it can be separated by the nature of the umbos which are flat in *fluctigera*. In addition, *fluctigera* possesses slightly serrated anterior and posterior dorsal margins and a larger shell.

The fossil lineage of *Tellina persica* begins in the Miocene of the Bowden formation of Jamaica. *Tellina hallistrepta* Dall from the Bowden is virtually indistinguishable from the modern species. *Tellina francisca* Olsson from the Esmeraldas formation at Punta Gorda, Ecuador, which is of Late Miocene–early Pliocene age and an unnamed fossil species from Miocene of Limon, Costa Rica also belongs to the lineage of *T.persica*.

This species seems to be most variable in the character of its margins. The anterior margin is narrowly rounded in adults while in immature stages it may be broadly rounded. The ventral margin which is convex in the adult stage seems to be straight in the smaller and younger individuals. The species tends to be a deeper water one, having been taken in 30–50 fathoms off Puerto Rico.

Range. This species, rare as it appears to be, possesses a range which extends from a northern limit off Matanzas, Cuba to a southern boundary at Tobago, Lesser Antilles.

Specimens examined. CUBA: *Atlantis* station 2999, off Bahia de Matanzas (23°10′ N; 81°11′ W), in 145–230 fathoms; *Atlantis* station 3332, off Bahia de Cochinos (22°09′ N; 81°11′ W), in 175–225 fathoms (both MCZ). PUERTO RICO: *Fish Hawk* station 6062, Mayaguez, in 30 fathoms; *Fish Hawk* station 6064, Mayaguez, in 33 fathoms; Johnson-Smithsonian station 104[1], off Salinas Island (18°30′ N; 66°13′ W), in 50 fathoms (all USNM). LESSER ANTILLES: $\frac{3}{4}$ mile S of Fort St. Louis, Fort de France, Martinique, in 14–16 fathoms; 2 miles S of Scarborough, in 36 fathoms (both MCZ).

Subgenus **Elliptotellina** *Cossmann*

Elliptotellina Cossmann, Annales Societé Royale Malacologique Belgique, **21:** 58, pl. 4, figs. 5–6 (type species, *Donax tellinella* Lamarck 1805, original designation).

Description. Shell small, elliptical, inaequilateral, equivalve, and with both ends rounded. Sculpture consisting of concentric ribs and radial lirations variously distributed on the surface. The ligament is small, strong and subtended by a well developed nymphal callosity. Hinge especially strong in the right valve; the right lateral teeth are subequal in strength and grooved above; the left lateral teeth are obsolete or absent. The pallial sinus is obliquely ascending and separated from the pallial line below except for an extremely short and posterior confluence.

The subgenus *Elliptotellina* was established for species occurring in the Eocene of the Paris Basin. Dall was the first to recognize the existence of two recent species in America. *Elliptotellina* is also represented in the Indo-Pacific by such species as *Tellina fabrefacta*

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[1] The published record for this station (Bartsch, 1933, p. 29) is "the depth ranged from 80–100 fathoms." The catalog in the USNM reads for station 104, 50 fathoms.

Pilsbry from Japan. In the Western Atlantic, the fossil record may be traced to the Miocene.

Tellina (Elliptotellina) americana *Dall*

Plate 149, fig. 6; Plate 155, fig. 4

Tellina (*Elliptotellina*) *americana* Dall 1900, Proc. U.S. Nat. Mus., **23:** 311, pl. 2, fig. 8 (*Albatross I* station 2612, off Cape Lookout, North Carolina (34°11′ N; 76°10′ W), in 52 fathoms) [holotype, USNM, no. 92154].

Description. Shell extending to 8.5 mm. (about 5/16 inch) in length and to 5.5 mm. (about 3/16 inch) in height, elliptical, solid, inflated with the valves of an equal convexity and with a slight posterior flexure. Umbos small and rounded. Anterior margin smoothly and narrowly rounded; ventral margin convex and rising gently posteriorly; anterior dorsal margin long and convex; posterior dorsal margin short and straight; posterior margin forming an oblique truncation. Concentric sculpture consisting of evenly spaced, raised and rounded ribs. Radial sculpture absent from the anterior slope and disc but markedly evident on the posterior slope. Ligament brown, short, protuberant and subtended by short nymphal callosities. In the left valve, the cardinal complex consists of an anterior strong bifid tooth with subequal lobes and a small, thin posterior laminate tooth; no true laterals developed. In the right valve, the cardinal complex consists of a posterior skewed bifid tooth with subequal lobes and an anterior strong laminate; anterior and posterior lateral teeth distal, strong and well developed. Both laterals set on a strong hinge plate with grooves above. Adductor muscle scars poorly impressed. Anterior and posterior adductors rounded and subequal. Pallial sinus extending straight out from the base of the posterior adductor, flattened above, rounded behind and falling obliquely and almost parallel to the pallial line; sinus is far removed from the anterior adductor scar; confluence short. Shell predominantly white or pale straw color with a crimson or brown spot on the dorsal margin near each end.

length	height	width	
8.5 mm.	5.5 mm.	3.2 mm.	Holotype of *americana* Dall
8.2	5.1	3.3	off Miami, Florida
6.9	4.5	3.5	Lantana, Florida
5.4	3.3	2.0	off Miami, Florida

Remarks. Tellina americana is the only member of the subgenus in the recent fauna of the Atlantic. Its nearest living relative is *T. pacifica* Dall of the Eastern Pacific. In *americana*, the radial sculpture is localized on the posterior slope only and the obliquely ascending pallial sinus is shorter than that of *pacifica* where the radial sculpture may extend far anteriorly. Woodring (1925) has described *T. cymobia* from the Miocene of Jamaica which is the precursor of the recent *Elliptotellina.*

Range. This species possesses a range which extends from off Cape Lookout, North Carolina south through the Florida Keys to a southernmost point off Barbados. It has also been found in the Gulf of Mexico, off Horn Island, Mississippi.

Specimens examined. North Carolina: *Albatross I* station 2612, off Cape Lookout (34°11′ N; 76°10′ W), in 52 fathoms (USNM). Florida: off Palm Beach; off Lantana, in 60 fathoms (both MCZ); off Miami, in 24–60 fathoms; off Fowey Light, in 25–70 fathoms; off Ajax Reef, in 40 fathoms; off Key West, in 90 fathoms; off Sand Key, in 30–100 fathoms (all USNM). Mississippi: Horn Island (ANSP). Lesser Antilles: off Lazaretto and off Pelican Island, Barbados, in 75–95 fathoms (both USNM).

Subgenus **Merisca** *Dall*

Merisca Dall 1900, Proc. U.S. Nat. Mus., **23**: 290 (type species, *Tellina crystallina* Wood 1815 (= *Tellina cristallina* Spengler 1798), original designation).

Lyratellina Olsson 1961, Panamic-Pacific Pelecypoda. Paleontological Research Inst., Ithaca, N.Y., p. 383 (type species, *Tellina lyra* Hanley 1844, original designation).

Description. Shell medium to small in size, trigonal-subovate-subquadrate in shape and partially rostrate posteriorly. Umbos centrally placed. Sculpture consisting of variously spaced and strong concentric lirations. Lateral teeth developed in the right valve. Lateral dentition of the left valve obsolete or totally lacking. Pallial sinus extensive and sometimes coalescing with the anterior adductor muscle scar. Confluence of the pallial sinus and the pallial line generally complete but rarely the pallial sinus may parallel the pallial line for some distance before becoming confluent with it. Generally the shell is dull white in color.

Merisca as defined and utilized herein may well constitute a heterogeneous but closely related assemblage of species. For example, *Merisca* closely approaches *Quadrans*, as represented in its type *Tellina gargadia* Linnaeus of the Indo-Pacific. In shell shape, concentric sculpture and in the development of the lateral dentition of the left valve, *Quadrans* possesses some differences to the Western Atlantic species of *Merisca*, *Tellina aequistriata* and *T. alerta*, which resemble it most closely. Likewise, *Tellina juttingae* might be compared to *Tellina lyra* Hanley and *T. lyrica* Pilsbry and Lowe from the Eastern Pacific, species for which Olsson (1961) erected the new genus, *Lyratellina*. The Eastern Pacific species have also been referred to Cossmann's *Macaliopsis*, which is based upon *Tellina barrandei* Deshayes, an Eocene species from the Paris Basin. Olsson considers the similarity of *Lyratellina* to *Macaliopsis* to be merely superficial. One of the major distinguishing traits of both *Lyratellina* and *Macaliopsis* is that the umbos are prosogyrous. However, the prosogyrate condition of the umbos is an inconstant trait and in such species as *Tellina martinicensis* of the Western Atlantic the umbos may vary in orientation from the orthogyrate to the prosogyrate position. *Merisca* is represented in the Atlantic, Pacific and Indian Oceans. Although a number of species extend into the more temperate zones, most are concentrated in the tropics. The group is well established in the Eocene.

KEY TO SPECIES OF *MERISCA* IN THE WESTERN ATLANTIC

1.	Right anterior lateral tooth subproximal to the cardinal complex	*cristallina*
	Right lateral teeth more or less equidistant from the cardinal complex	2
2.	Pallial sinus extending parallel to the pallial line for about half its length before becoming confluent	3
	Pallial sinus uniting with the pallial line without paralleling it	4
3.	Anterior dorsal margin short and deeply concave	*juttingae*
	Anterior dorsal margin long and weakly concave	*martinicensis*
4.	Pallial sinus uniting with the pallial line very near the base of the anterior adductor muscle scar	*aequistriata*
	Pallial sinus well removed from the anterior adductor muscle scar and uniting with the pallial line in the posterior portion of the valve	*alerta*

Tellina (Merisca) cristallina *Spengler*
Plate 138, fig. 5; Plate 139, fig. 6

Tellina cristallina Spengler 1798, Skrivter Naturhistorie Selskabet, **4**(2): 113 (Newport, Long Island) [type locality, here corrected, St. Thomas, Virgin Islands; holotype, Zoological Museum, Copenhagen].

Tellina crystallina Wood 1815, General Conchology, p. 149 (no locality given) [refers to Chemnitz, Conch. Cab. (1), **11**: 210, pl. 199, fig. 1947, 1948].

Tellina schrammi Récluz 1853, Jour. de Conchy., **4**: 152, pl. 6, figs. 7–8 (Point-a-Pitre, Guadeloupe) [types not seen].

Tellina (*Merisca*) *crystallina* Wood. Dall 1900, Proc. U.S. Nat. Mus., **23**: 293.

Tellina (*Merisca*) *cristallina* Spengler, Warmke and Abbott 1961, Caribbean Seashells, p. 196, pl. 40, fig. b.

Description. Shell extending to 24 mm. (about 1 inch) in length and to 18 mm. (about $\frac{3}{4}$ inch) in height, ovate-subtrigonal, produced posteriorly, rather compressed with the left valve somewhat convex and the right valve concave or flattened and with a strong and marked posterior flexure to the right. Umbos central and conspicuous. Anterior margin broadly rounded; ventral margin convex and rising posteriorly; anterior and

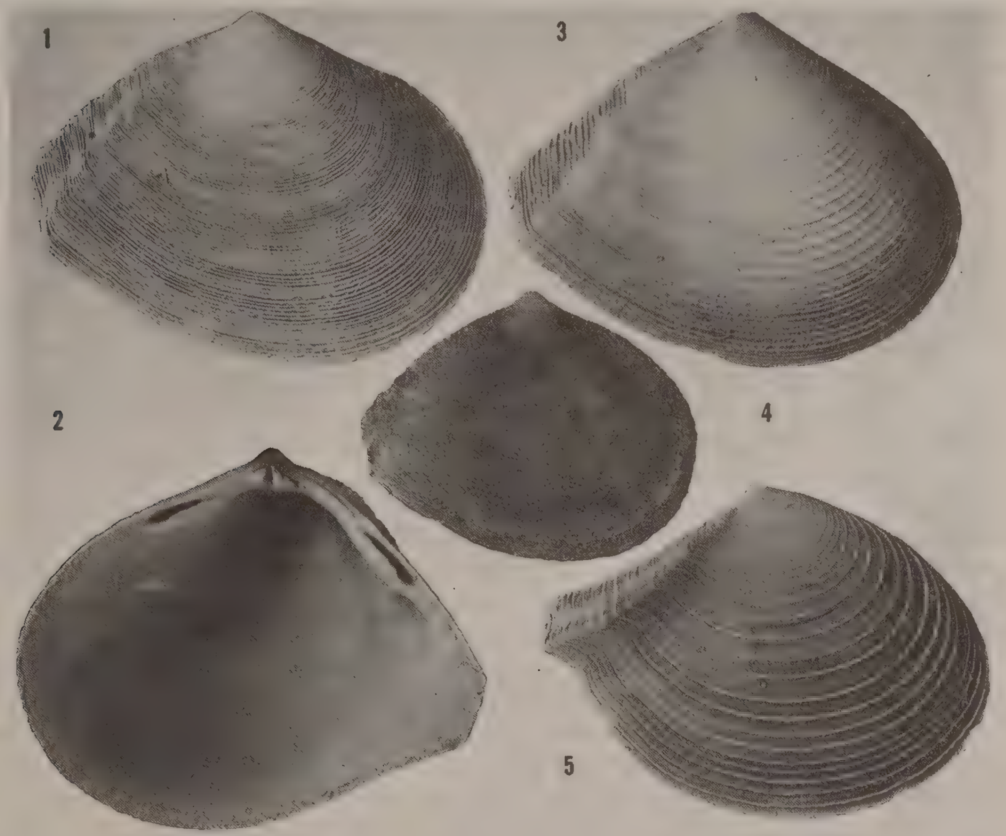

Plate 138. Figs. 1–4. *Tellina martinicensis* d'Orbigny. Fig. 1. External view of the right valve, Tobago, West Indies, MCZ 243067 (about 5.8x) [L=12 mm.]. Fig. 2. Internal view of the right valve, Puerto Rico, MCZ 243128 (about 6.4x) [L=11 mm.]. Fig. 3. External view of the right valve, Puerto Rico, MCZ 243128 (about 8x) [L=8.5 mm.]. Fig. 4. External view of the right valve of a syntype, Martinique, BMNH (about 6x) [L=7.5 mm.]. Fig. 5. *Tellina cristallina* Spengler, external view of the right valve, Bahia Bramadero, Puerto Rico, MCZ 243127 (about 3x) [L=24 mm.].

posterior dorsal margin long and steeply descending; posterior margin short, straight and giving the shell a truncate appearance. Sculpture consisting of strong, widely spaced concentric ridges separated by broad flattened bands; no true radial sculpture evident. Posterior ridges and sulci in both valves. Ligament brown and somewhat sunken. Calcareous element of the ligament small and not supported by a raised nymphal callosity. In the left valve, the cardinal complex consists of an anterior, narrow and elongate bifid tooth, with the anterior lobe the larger and of a posterior and elongate laminate tooth; anterior lateral tooth weak, obsolete and subproximal to the cardinal complex; posterior lateral stronger, thin and distal to the cardinal complex. In the right valve, the cardinal complex consists of a posterior elongate, slightly skewed bifid tooth with the anterior lobe the larger and of an anterior long laminate tooth; the anterior lateral tooth is subproximal to the cardinal complex, rather well developed, but weaker than the distal posterior lateral tooth. Adductor muscle scars poorly impressed. Anterior adductor elongate, narrow and lunate; posterior adductor irregularly circular. Pallial sinus dissimilar in opposite valves, generally rising to an apex, descending gently and uniting with the pallial line close to the anterior adductor. The shell is thin, rather opaque, lustreless and white.

length	height	width	
24 mm.	18 mm.	—	Cartagena, Colombia
24	17	6 mm.	St. Thomas
22	16	5	Barcelona Beach, Venezuela
12	8	—	Baie Anglaise, Haiti

Remarks. The holotype of *Tellina cristallina* Spengler consists of a broken right valve and is preserved in the Zoological Museum of Copenhagen, The type locality originally given was Newport, Long Island [Rhode Island] and is in error since the species does not range that far north. In all probability, the original specimen came from the then Danish West Indies and for this reason, the type locality is here corrected to St. Thomas. Virgin Islands. Some early workers considered that this species was Eastern Pacific whereas Dall (1900a) contended that it was distributed in both the Atlantic and the Pacific. Recently Olsson (1961) has considered the problem and arrived at a satisfactory result, for he has been able to separate a distinct Eastern Pacific analog of *cristallina*. In contrast to *Tellina* (*Merisca*) *rhynchoscuta* Olsson of the Eastern Pacific, *cristallina* may be distinguished by its straight anterior and posterior dorsal margins. Olsson has also noted that *rhynchoscuta* has heavier, more stubby valves, stronger and coarser concentric sculpture and a deeper sulcus which extends in front of the rostral ridges.

Tellina cristallina has been discovered in the Pliocene and Miocene strata of the Western Atlantic. Maury (1917) has documented its occurrence in the Miocene of Santo Domingo. *Tellina sancti-dominici*, closely allied to *cristallina* but no longer living in the modern fauna, was also described by Maury from the Miocene of Santo Domingo. According to Hertlein and Strong (1949), Lynge (1909) described an Indo-Pacific species, *Tellina martensi*, which may be distinguished from *cristallina* by its less rostrate shell; unfortunately no specimens of *martensi* have been available for study.

Range. This species ranges from Sullivan's Island, South Carolina through the Greater Antilles and Virgin Islands. It also occurs on the eastern coast of Central America and on the northern coast of South America.

Specimens examined. SOUTH CAROLINA: Sullivan's Island (USNM). GUATEMALA: (BMNH). JAMAICA: Black River, St. Elizabeth (USNM). HISPANIOLA. HAITI: Jerémié; Baie Anglaise (both USNM). SANTO DOMINGO: Monte Cristi; Puerto Plata (both MCZ). PUERTO RICO: Bahia Bramadero (IMPBR). VIRGIN ISLANDS: St. Thomas (USNM). COLOMBIA: Cartagena (MCZ). VENEZUELA: Barcelona (USNM); Margarita Island (ANSP).

Tellina (Merisca) martinicensis *d'Orbigny*

Plate 138, figs. 1–4; Plate 139, fig. 5

Tellina martinicensis d'Orbigny 1942 [in] Sagra, Hist. L'Ile Cuba, Atlas, pl. 26, figs. 6–9; 1845, Spanish Text, **2**(5): 305; (Martinica y la Guadalupe); 1853, French Text, Mollusques, **2**: 253 [type locality, here restricted, Martinique; syntypes, BMNH, no. 54.10.4.511].

Tellina (Moerella) martinicensis d'Orbigny. Dall, 1900 Proc. U.S. Nat. Mus., **23**: 295.

Tellina (Moerella) obtusa 'Sowerby' Dall 1900, Proc. U.S. Nat. Mus., **23**: 295, *non* Sowerby 1817, *nec* Sowerby 1868.

Tellina (Moerella) tumida 'Sowerby' Dall 1900, Proc. U.S. Nat. Mus., **23**: 295, *non* Sowerby 1867.

Tellina (Tellinella) versluysi Dautzenberg 1900, Mem. Soc. Zool., Paris, **13**: 115, pl. 10, fig. 5 (Santa Marta Colombia; syntypes, Dautzenberg collection, Institut Royal des Sciences Naturelles, Bruxelles).[1]

Tellina (Eurytellina) martinicensis d'Orbigny. Dall and Simpson 1901, Bull. U.S. Fish. Comm., **20**(1): 480.

Tellina (Merisca) martinicensis d'Orbigny. Warmke and Abbott 1961, Caribbean Seashells, p. 196, pl. 40 i.

Description. Shell extending to 12.2 mm. (about ½ inch) in length and to 10.1 mm. (about ⅜ inch) in height, ovate, solid, slightly produced posteriorly, inflated with valves of equal convexity and with a strong posterior flexure to the right. Umbos subcentral, inflated and blunt. Anterior margin broadly rounded; ventral margin convex and with a strong postbasal arcuation; anterior dorsal margin gently sloping and straight; posterior dorsal margin long, steeply sloping and convex; posterior margin short, straight and forming an oblique truncation. Sculpture consisting of raised and strong concentric ridges (about 4 per millimeter) separated by broad bands. No radial sculpture. Ligament brown, inconspicuous and sunken; no true nymphal callosities. In the left valve, the cardinal complex consists of an anterior strong bifid tooth with subequal lobes and of a posterior protuberant laminate tooth; both lateral teeth consisting of localized thickenings of the hinge plate. In the right valve, the cardinal complex consists of a posterior strong bifid tooth with subequal lobes and of an anterior thickened laminate tooth; both laterals strong. Adductor muscle scars not well impressed. The anterior adductor elongate and narrow; posterior adductor rounded. Pallial sinus more or less equal in both valves, rising high posteriorly, rounded and extending far anteriorly, nearly to the anterior adductor scar, arcuate ventrally and extending parallel to the pallial line for nearly one half its ventral length; confluence short. Shell white and rarely iridescent.

length	height	width	
12.2 mm.	10.1 mm.	—	Santa Lucia, Cuba
10.0	8.5	5.5 mm.	Florida
9.0	7.0	4.0	Mayaguez, Puerto Rico
8.1	6.4	3.2	Bahia de Samana, Santo Domingo

Remarks. In the Western Atlantic, *Tellina martinicensis* appears to be most closely related to the rare *Tellina juttingae.* It never attains the great size exhibited by *juttingae,* which appears to be four or five times greater in its dimensions. In addition, the anterior dorsal margin of *juttingae* is strongly convex and the umbo appears to be prosogyrous, although this latter characteristic appears rarely in *martinicensis.*

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[1] The author is indebted to Dr. C. O. van Regteren Altena of the Rijksmuseum van Natuurlijke Historie, Leiden for checking the syntypes of the Dautzenberg species.

Tellina aequistriata Say may be confused with *martinicensis;* however, in the latter, the shell is more tumid, the umbos higher, and the concentric sculpture stronger. The

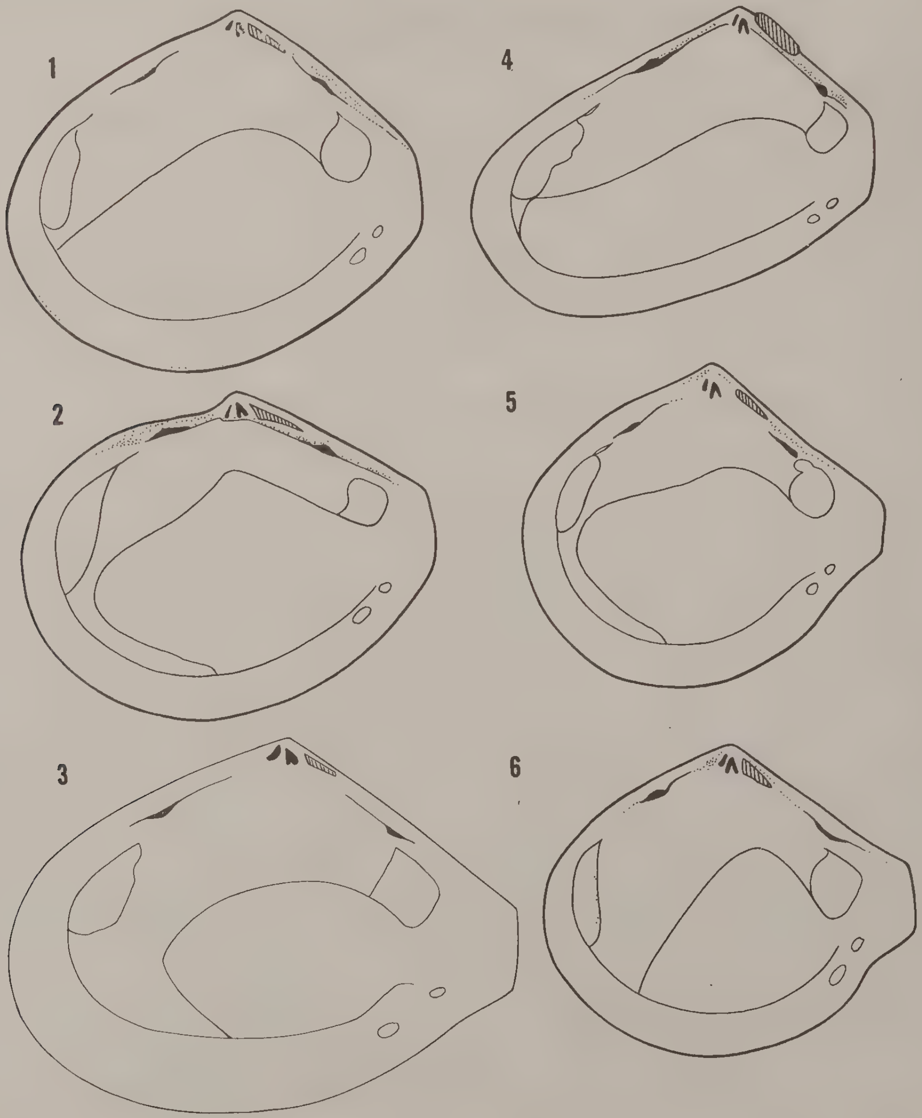

Plate 139. Figs. 1–6. Diagrammatic illustration of the internal surface of the right valve showing the dental configuration and muscle scars. Fig. 1. *Tellina aequistriata* Say (about 3x) [L=21 mm.]. Fig. 2. *Tellina juttingae* Altena (about 3x) [L=22 mm.]. Fig. 3. *Tellina alerta* Boss (about 10x) [L=8 mm.]. Fig. 4. *Tellina gouldii* Hanley (about 7x) [L=9 mm.]. Fig. 5. *Tellina martinicensis* d'Orbigny (about 4.5x) [L=12 mm.]. Fig. 6. *Tellina cristallina* Spengler (about 4.4x) [L=20.].

species are distinct with regard to the pallial sinus. In *martinicensis*, the sinus unites with the pallial line posteriorly and in *aequistriata* it is confluent at or near the base of the anterior adductor muscle scar.

The earliest precursor to *Tellina martinicensis* occurs in the Miocene of the Bowden marls of Jamaica. Woodring (1925) has described *Tellina sclera lerasca* which exhibits a similarity of dentition, sculpture and tumidity. The recent species is also represented by *Tellina caloosana* in the Pliocene of the Caloosahatchee in Florida (Dall, 1900b). In the Eastern Pacific, *Tellina proclivis* Hertlein and Strong appears to be the analog of *Tellina martinicensis.*

Range. This species is found from Tampa Bay, Florida south through the Greater and Lesser Antilles to Scarborough, Tobago.

Specimens examined. Florida: off Main Channel, Key West, in 10–20 fathoms; Western Dry Rocks (both MCZ); Tortugas, in 15 fathoms (USNM); Gulfport, Tampa Bay (ANSP). British Honduras: Belize; Monkey River (both ANSP). Panama: Mt. Hope (Pleistocene, ANSP). Cuba: *Barrera* station 209, Santa Rosa, in 3–6 fathoms; *Barrera* station 200, Santa Lucia, in 2–4 fathoms; *Barrera* station 208, Bahía Honda, in 1–12 fathoms; *Barrera* station 203, Cabanas Harbor, in 3–12 fathoms; *Barrera* station 212, Cardenas Bay, in 1–3 fathoms (all USNM). Jamaica: (MCZ). Hispaniola. Santo Domingo: Puerto Plata (ANSP); Santa Barbara de Samana (USNM). Puerto Rico: Mayagüez; off Enrique Reef, La Parguera, in 30–75 feet (both IMPBR); San Juan Harbor, in 5 fathoms (USNM). Virgin Islands: St. Thomas (ANSP). Lesser Antilles: $\frac{3}{4}$ mile S of Fort St. Louis, Martinique (MCZ); Carlisle Bay, Barbados, in 12 fathoms (USNM); 2 miles S of Fort George, Scarborough, Tobago (MCZ).

Tellina (Merisca) juttingae *Altena*

Plate 139, fig. 2; Plate 140, figs. 1–2

Lyratellina juttingae Altena 1965, Basteria, **29**: 52–54, figs. 1a–e (N of the mouth of the Surinam River, 20 miles off the coast, at 15 fathoms; holotype, Rijksmuseum van Natuurlijke Historie, Leiden).

Description. Shell extending to 28.5 mm. (about $1\frac{1}{8}$ inches) in length and to 21 mm. (about 3.4 inches) in height, elongate-subquadrate, with both valves of more or less equal convexity and with a very weak flexure to the right. Umbos subcentral, prosogyrous and pointed. Anterior margin broadly rounded; ventral margin broadly arcuate and rising posteriorly; anterior dorsal margin falling abruptly from the umbonal region and distinctly concave; posterior dorsal margin rather steeply inclined and long; posterior margin short and straight, forming a blunt truncation. Sculpture consisting of broadly and evenly spaced slightly raised ridges (2–4 per millimeter), separated by broad flat bands; no radial sculpture. Ligament not observed; no nymphal callosities. In the left valve, the cardinal complex consists of an anterior small and weak bifid tooth with subequal lobes and of a posterior thin laminate tooth; no true anterior lateral tooth; posterior lateral absent or obsolete. In the right valve, the cardinal complex consists of a posterior, small subdeltoid bifid tooth with the posterior lobe the larger and of an anterior thickened laminate tooth; anterior and posterior lateral teeth well developed, distal to the cardinal complex, subequal in strength and with sockets above. Adductor muscle scars moderately impressed. Anterior adductor scar elongate and narrow; posterior adductor transversely quadrate. Pallial sinus extensive, rising abruptly behind, extending in a broad arcuation anteriorly but not touching the anterior scar; the sinus parallels the pallial line ventrally and unites posteriorly; confluence short. Shell white, partly covered with an olivaceous gray periostracum, rarely iridescent.

length	width	
28.5 mm.	21 mm.	Trinidad
25.5	19	"
23.0	17	"
22.5	16	"

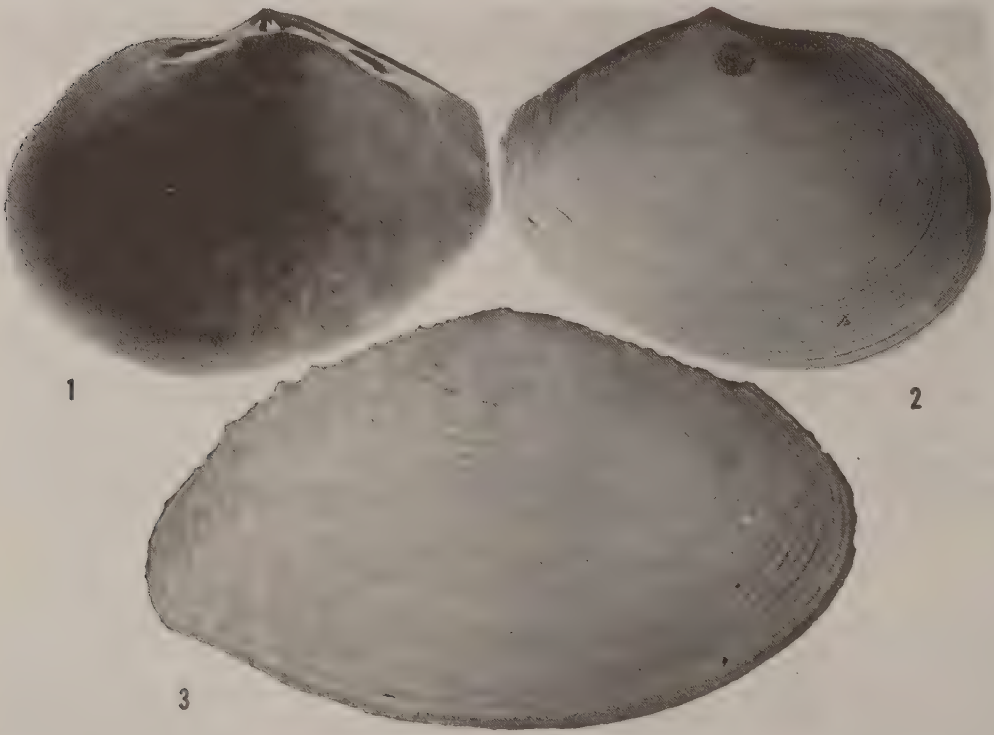

Plate 140. Figs. 1–2. *Tellina juttingae* Altena. Fig. 1. Internal view of the right valve, Trinidad, MCZ 239112 (about 3.4x) [L=22.5 mm.]. Fig. 2. External view of the right valve, Trinidad, MCZ 239112 (about 3.4x) [L=23 mm.]. Fig. 3. *Tellina squamifera* Deshayes, external view of the right valve of the holotype, 'Chinese Seas', BMNH (about 5.5x) [L=20.8 mm.].

Remarks. This species is extremely rare. The shell is rather thin, rounded in front, and bluntly truncated behind; the peculiar shape of the anterior dorsal margin is certainly diagnostic. Of the Western Atlantic tellins, *Tellina martinicensis* is most closely related. The dentition, the external sculpture and the configuration of the pallial sinus in *martinicensis* are quite similar to *juttingae;* however, *juttingae* attains a much greater size. In contrast to *juttingae*, the shell is thicker, the postbasal arcuation stronger and the posterior truncation shorter in *martinicensis. Tellina lyra* Hanley is the Eastern Pacific analog of *juttingae.*

Range. This species occurs from off Surinam to Trinidad.

Specimens examined. TRINIDAD: Saut d'Eau Bay, in 10–20 fathoms (MCZ). SOUTH AMERICA: N of the mouth of the Surinam River (Rijksmuseum, Leiden).

Tellina (Merisca) aequistriata *Say*

Plate 139, fig. 1; Plate 141, figs. 1–2; Plate 142, figs. 1–3

Tellina aequistriata Say 1824, Jour. Acad. Nat. Sci., Philadelphia, **4:** 145, pl. 10, fig. 7 (Maryland, Miocene) [types lost], *non* Sowerby 1868.

Tellina lintea Conrad 1837, Jour. Acad. Nat. Sci., Philadelphia, **7:** 259, pl. 20, fig. 3 (Mobile Point, Alabama) [types lost], *non* Conrad 1848, *nec* Hutton 1873.

Tellina guadaloupensis d'Orbigny 1842 [in] Sagra, Hist. L'Ile Cuba, Atlas, pl. 26, figs. 1–3 (Guadeloupe) [holotype, BMNH, no. 54.10.4.508].

Tellina guadalupensis d'Orbigny 1845 [in] Sagra, Hist. Isla Cuba, Spanish Text, **2**(5): 304, error for *guadaloupensis* d'Orbigny.

Tellina guadalupiensis d'Orbigny 1853 [in] Sagra, Hist. L'Ile Cuba, Mollusques, French Text, **2:** 253, error for *guadaloupensis* d'Orbigny.

Tellina tumida Sowerby 1867 [in] Reeve, Conch. Icon., **17, Tellina,** pl. 23, figs. 120a and b (Jamaica) [holotype, BMNH, no. 67.10.7.18].

Tellina (Tellinella) ostracea 'Lamarck' Dautzenberg 1900, Mem. Soc. Zool., Paris, **13:** 259, *non* Lamarck 1818.

Tellina (Merisca) aequistriata Say. Dall 1900, Trans. Wagner Free Inst. Sci., Philadelphia, **3**(5): 1020.

Tellina (Merisca) lintea Conrad. Dall 1900, Proc. U.S. Nat. Mus., **23:** 293.

Quadrans lintea Conrad. Warmke and Abbott 1961, Caribbean Seashells, p. 198, pl. 41 k.

Description. Shell extending to 24.5 mm. (about 1 inch) in length and to 19 mm. (about $\frac{3}{4}$ inch) in height, subrhomboid, produced behind, subsolid, with the left valve markedly more convex and with a strong, sharp posterior flexure to the right. Umbos nearly central and pointed. Anterior margin broadly rounded; ventral margin arcuate, convex and rising posteriorly; anterior dorsal margin long and gently sloping; posterior dorsal margin straight and steeply inclined; posterior margin short, straight and forming a truncation. Sculpture consisting of raised, more or less sharp and evenly spaced concentric ridges (4–8 per millimeter), separated by rather broad sulci; no radial sculpture. Ligament light yellow to dark brown, inconspicuous and sunken. Calcareous element of the ligament short and resting on the flattened hinge plate; no true nymphal callosities. In the left valve, the cardinal complex consists of an anterior elongate bifid tooth with thin subequal lobes and of a posterior elongate and somewhat curved laminate tooth; both lateral teeth poorly developed, posterior one distal. In the right valve, the cardinal complex consists of a posterior elongate strong bifid tooth with subequal lobes and of an anterior elongate and thickened laminate tooth; the lateral teeth strong, distal to the cardinal complex and socketed. Adductor muscle scars well impressed. Anterior adductor dorsoventrally elongate and lunate; posterior adductor quadrate. Pallial sinus equal in opposite valves, rising abruptly behind, rounded above, descending gently without an anterior arcuation and uniting with the pallial line just beneath the anterior adductor scar; confluence entire. Shell white, sometimes covered by an adhering brownish periostracum.

length	height	width	
9.5 mm.	6.9 mm.	3.3 mm.	Holotype of *guadaloupensis* d'Orb.
24.5	19.0	—	off Cape Hatteras, North Carolina
16.0	11.5	6.0	Pass Cabello, Texas
4.6	3.1	—	Matanzas Bay, Cuba

Remarks. The fossil history of *Tellina aequistriata* extends back to the Miocene and there are ample records of the occurrence of this species in North American strata. Dall (1900b) and Mansfield (1932) have documented the fossil records for this species from Virginia, North Carolina, South Carolina and Florida. In addition, Woodring (1925) has listed *Tellina acrocosmia* Dall, which is a predecessor of *Tellina aequistriata*, from the Bowden marls of Jamaica.

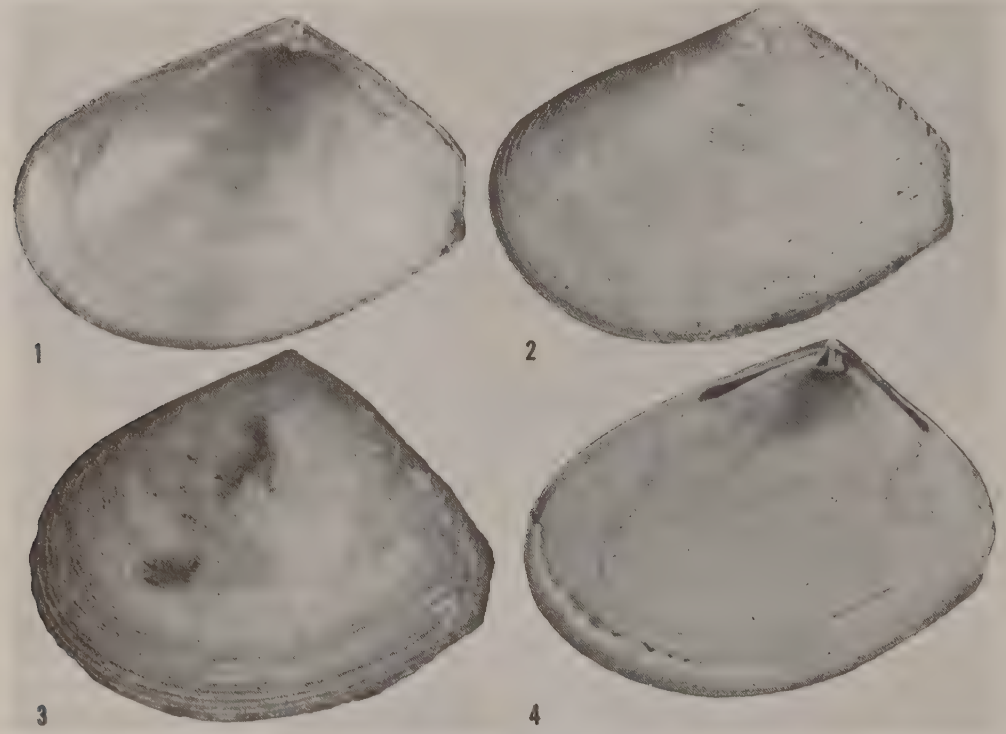

Plate 141. Figs. 1–2. *Tellina aequistriata* Say. Fig. 1. Internal view of the right valve. Fig. 2. External view of the right valve, Red Fish Pass, Captiva, Florida, MCZ 236307 (about 5x) [L = 15.5 mm.]. Figs. 3–4. *Tellina alerta* Boss. Fig. 3. Internal view of the right valve of the paratype (about 9x) [L = 8.3 mm.]. Fig. 4. External view of the left valve of the holotype, 32°45′ S; 50°39′ W, BMNH (about 9x) [L = 8 mm.].

Heretofore, *Tellina aequistriata* Say and *T. lintea* Conrad have been maintained as separate entities but there are no morphological differences which can distinctly separate *aequistriata* into two species. Dall (1900b) noted that equal sized specimens were not divisible into separate species but he maintained that a difference of proportions was evident in adults. The differences of proportions in *aequistriata* are amply exhibited in any sizable sample from a population.

The near allies, *Tellina martinicensis* and *T. juttingae* are distinguished from *T. aequistriata* by the short confluence of the pallial line and the pallial sinus. *Tellina alerta* is the nearest relative of *T. aequistriata*, but in *alerta* the pallial sinus is widely separated from the anterior adductor muscle scar and the periostracum is dull red-brown. In the Eastern Pacific, the analog of *T. aequistriata* is *T. reclusa* Dall, which may be distinguished by its shorter more trigonal shape and its rasplike sculpture.

According to Parker (1960, p. 323), *Tellina aequistriata* is characteristically a member of the sandy bottom community along the intermediate shelf in the Gulf of Mexico at depths from 12–35 fathoms.

Range. This species is found from off Beaufort, North Carolina south throughout the Bahama Islands, the Greater and Lesser Antilles to off Bahia, Brasil.

Specimens examined. NORTH CAROLINA: Beaufort; off Cape Hatteras, in 9–22 fathoms; Pivers Island (all USNM). SOUTH CAROLINA: Sullivan's Island (CM). FLORIDA: Lake Worth; off Miami; off Caesar's Creek Bank; off Pacific Reef; Key Largo; Sombrero Key; Looe Key (all MCZ); Key West; Charlotte Harbor; Sarasota; Cedar Keys (all USNM); Destin; Pensacola (both MCZ). ALABAMA: Fort Morgan (MCZ). MISSISSIPPI: Horn Island (ANSP). TEXAS: Pass Cabello. MEXICO: Veracruz; Yucatan (both MCZ). GUATEMALA: Puerto Barrios (ANSP). BAHAMA ISLANDS: Little Abaco (MCZ); off North Bimini Island, in 20 fathoms (USNM); New Providence (MCZ); off Green Cay, in 9 fathoms (USNM). CUBA: *Barrera* station 211, Cape Cajon; *Barrera* station 209, Santa Rosa, in 3–6 fathoms; *Barrera* station 200, Santa Lucia, in 2–4 fathoms; *Barrera* station 204, Cayo Arenas, in 2 fathoms; *Barrera* station 208, Bahía Honda, in 1–12 fathoms; *Barrera* station 202, Cabanas Harbor, in 25 fathoms (all USNM); Matanzas Bay; Rio Arimas (both MCZ); off Isle of Pines, in 3 fathoms (USNM). JAMAICA: Montego Bay (USNM). HISPANIOLA. HAITI: Jerémié (USNM). PUERTO RICO: off Mayagüez, in 30 fathoms (USNM); off Enrique Reef, La Parguera, in 30–75 feet (IMPBR). VIRGIN ISLANDS: Charlotte Amalie, St. Thomas, in 30 feet (ANSP). LESSER ANTILLES: English Harbour, Antigua, in 7 fathoms (USNM); $\frac{3}{4}$ mile S of Fort St. Louis, Martinique (MCZ); Carlisle Bay, Barbados, in 6–12 fathoms (USNM); 2 miles S of Fort George, Scarborough, Tobago, in 36 fathoms (MCZ). CARIBBEAN ISLANDS: off the Stack, Georgetown, Grand Cayman Island, in 8 fathoms (ANSP). BRASIL: *Albatross I* station 2758, 34 miles SE of Natal (06°59′ S; 34°47′ W), in 20 fathoms (USNM); off Bahia (11°49′ S; 37°27′ W), in 12 fathoms (MCZ).

Tellina (Merisca) alerta *Boss*

Plate 139, fig. 3; Plate 141, figs. 3–4

Quadrans lintea 'Conrad' Richards and Craig, 1963, Proc. Acad. Nat. Sci. Philadelphia, **115**: 135, pl. 1, figs. 8, 8, *non* Conrad 1837.

Tellina (Merisca) alerta Boss 1964, Occ. Pap. Dept. Mollusks, Harvard University, **2**: 309, pl. 55, figs. 1–2 (about 15 miles SE of Rio Grande do Sul, Brasil, in 48 fathoms (32°45′ S; 50°39′ W); holotype, BMNH, no. 79.10.15.171.2).

Description. Shell extending to 8.2 mm. (about 5/6 inch) in length and to 6.5 mm. (about 1/4 inch) in height, elongate-subtrigonal, subsolid to thin, a little tumid with the left valve more convex and with a sharp flexure to the right posteriorly. Umbos central and pointed. Anterior margin smoothly rounded; ventral margin gently convex and rising in a concave basal arcuation posteriorly; anterior dorsal margin straight and gently inclined; posterior margin short, parallel with the dorso-ventral axis and forming a blunt truncation. Sculpture consisting of regularly spaced, raised lamellae (about 10–12 per millimeter) separated by sulci. Ligament light brown and slightly protuberant. Calcareous portion of the ligament poorly developed. In the left valve, the cardinal complex consists of an anterior subdeltoid tooth with subequal lobes and of a posterior extremely elongate laminate tooth; distal anterior and posterior lateral teeth present, protruding and weak. In the right valve, the cardinal complex consists of a posterior thickened bifid tooth with subequal lobes and of an anterior subdeltoid laminate tooth; distal anterior and posterior lateral teeth present, elongate, strong upcurled and socketed. Adductor muscle scars well impressed. Anterior adductor scar elongate, pointed above and rounded below; posterior adductor scar subquadrate. Pallial sinus equal in opposite valves, rising gently behind, widely separated from the anterior adductor scar and forming a short confluence posteriorly. Periostracum dull reddish-brown, the external surface of the valves eroded in the umbonal region and the remainder a dull white.

length	height	width	
8.3 mm.	6.5 mm.	3.0 mm.	Paratype of *alerta*
8.0	6.0	2.8	Holotype of *alerta*

Remarks. *Tellina alerta* is most closely allied to *Tellina aequistriata.* The shape of the shell, the concentric sculpture and the configuration of the lateral teeth of the right valve serve to indicate the close relationship between these species. The pallial sinus is the most important character used to distinguish the species. In *aequistriata*, the sinus falls to and is confluent with the pallial line at or very near the base of the anterior adductor muscle scar while in *alerta* it is widely separated from the anterior adductor scar and the confluence of the sinus and the pallial line is short. *Tellina alerta* possesses a dark periostracum which differs from the white periostracum of *aequistriata*, and the lateral compression of the valves appears to be greater in *alerta.*

Range and specimens examined. This species is known from the type locality and from off Uruguay (34°47′ S; 52°47′ W) in 54.9 meters as figured by Richards and Craig (1963).

Subgenus **Acorylus** *Olsson and Harbison*

Acorylus Olsson and Harbison 1953, Acad. Nat. Sci., Philadelphia, Monograph 8, p. 128 (type species, *Tellina suberis* Dall 1900, original designation).

Description. Shell small, solid, obliquely subovate, with a right posterior flexure. Hinge line strong and heavy. Two strong lateral teeth in the right valve, equidistant from the cardinal complex and socketed. No true lateral teeth in the left valve. Pallial sinus large, reaching to the anterior adductor muscle scar and extensively confluent with the pallial line.

Acorylus is employed herein as described by Olsson and Harbison (1953). *Morella* with *Tellina donacina* Linnaeus as type is closely allied but differs in the increased strength of its concentric sculpture and the protuberant nature of the right lateral dentition. *Cadella*, a genus of Dall, Bartsch, and Rehder, with the Indo-Pacific *Tellina lechiogramma* Melville as type, is also close to *Acorylus*, but *Cadella* has a stronger sculpture and the confluence of the pallial line and the pallial sinus is not extensive.

Acorylus is monotypic in the recent fauna of the Western Atlantic.

Tellina (Acorylus) gouldii *Hanley*

Plate 139, fig. 4; Plate 142, fig. 4

Tellina cuneata d'Orbigny 1842 [in] Sagra, Hist. L'Ile Cuba, Atlas, pl. 26, figs. 21–23; 1845, Spanish Text, 2(5): 306 (Cuba y a las Floridas); 1853, French Text, Mollusques, 2: 256 [type locality, here restricted, Habana, Cuba; holotype, BMNH, no. 54.10.4.5.2], *non* Spengler 1798.

Tellina gouldii Hanley 1846 [in] Sowerby, Thesaurus Conchyliorum, **1:** 272, pl. 56, fig. 26 (West Indies) [type locality, here restricted, Habana, Cuba; holotype, BMNH], *non* Carpenter 1864.

Tellina (*Moera*) *gouldii* Hanley. H. and A. Adams 1856, Genera Recent Mollusca, **2:** 396.

Tellina (*Acorylus*) *gouldii* Hanley. Olsson and Harbison 1953, Acad. Nat. Sci., Philadelphia, Monograph 8, p. 128.

Tellina (*Moerella*) *cuneata* d'Orbigny. Abbott 1958, Acad. Nat. Sci., Philadelphia, Monograph 11, p. 134, pl. 5 j and k, map 8.

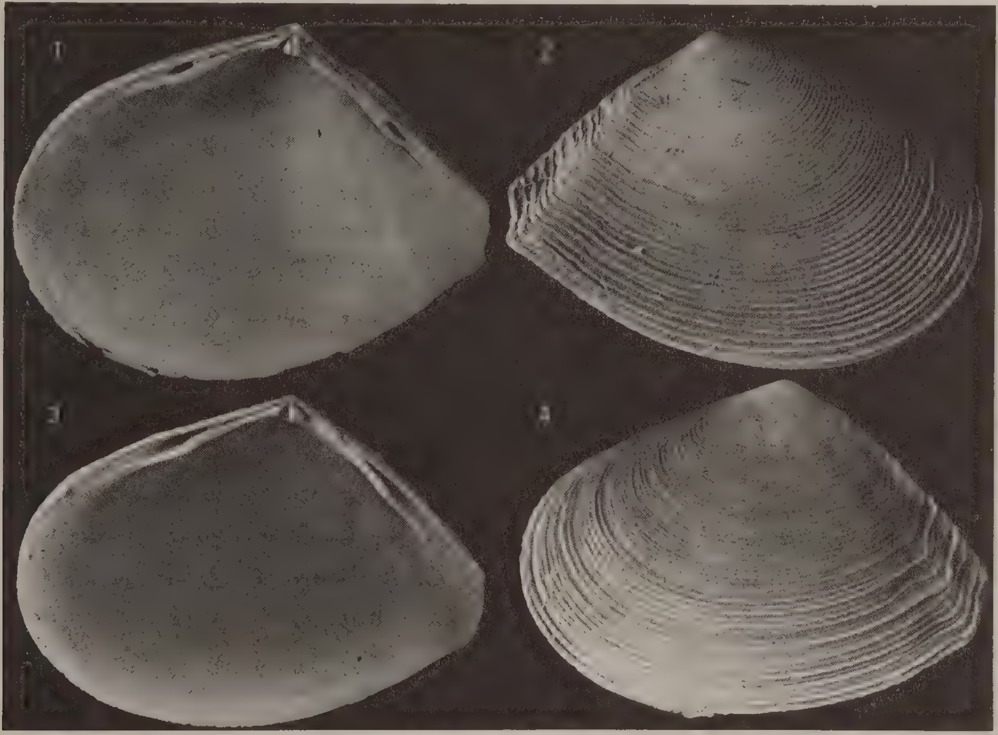

Plate 142. Figs. 1–2. *Tellina guadaloupensis* d'Orbigny [= *Tellina aequistriata* Say]. Fig. 1. Internal view of the right valve of the holotype. Fig. 2. External view of the left valve of the holotype, Guadeloupe, West Indies, CMNH (about 7x) [L=9.5 mm.]. Fig. 3. *Tellina tumida* Sowerby [= *Tellina aequistriata* Say], external view of the left valve of the holotype, Jamaica, BMNH (about 9x) [L=8.7 mm.]. Fig. 4. *Tellina gouldii* Hanley, internal view of the right valve, Bermuda, MCZ 243073 (about 8x) [L=9.5 mm.].

Description. Shell extending to 10.3 mm. (about $\frac{3}{8}$ inch) in length and to 7.8 mm. (about $\frac{1}{4}$ inch) in height, solid, heavy, obliquely subovate and with a very slight flexure to the right posteriorly. Umbos posterior to the middle, somewhat elevated and rounded. Anterior margin narrowly rounded; ventral margin convex and gently rising posteriorly; anterior dorsal margin long, straight and steeply sloping; posterior dorsal margin short and steep; posterior margin short and forming a truncation. Sculpture consisting of weak concentric lirations; obsolete radial sculpture sometimes evident. Ligament light golden-brown or yellow, not prominent and deeply set. In the left valve, the cardinal complex consists of an anterior small bifid tooth with subequal lobes and of a posterior thin laminate tooth; lateral teeth obsolete. In the right valve, the cardinal complex consists of a posterior deltoid bifid tooth with subequal lobes and of an anterior thin laminate tooth; lateral teeth equidistant from the cardinal complex, strong and socketed. Adductor muscle scars fairly well impressed. Anterior adductor lunate; posterior adductor large and ovate. Pallial sinus rising abruptly, descending arcuately and touching the anterior adductor scar; confluence nearly entire. Shell white internally and externally; rarely iridescent.

length	height	width	
8.7 mm.	6.7 mm.	3.3 mm.	Holotype of *gouldii* Hanley
7.2	5.5	3.0	Holotype of *cuneata* d'Orb.
10.3	7.2	4.2	Bailey's Bay, Bermuda
9.2	7.8	4.1	Long Island, Bahamas
4.7	3.6	1.7	Grand Cayman Island

Remarks. This is a distinctive species whose small size and characteristic shape serve to distinguish it from other *Tellina*. The ancestors of *gouldii* are well represented in the Tertiary of North America and the Caribbean. The immediate predecessor to *gouldii* is *suberis* Dall from the Pliocene of Caloosahatchie, Florida. The species *gouldii* stands rather alone in its distant relationship to the other *Tellina* in the Western Atlantic and for that reason the subgeneric position given it by Olsson and Harbison is adopted.

In shape, *gouldii* might be confused with *Tellina candeana* d'Orbigny, but the latter may be immediately identified by its scissulate sculpture. Also, *gouldii* may be confused with *Semele nuculoides* Conrad, but the latter is distinguished by its internal ligament, its distinct escutcheon and its free pallial sinus.

Tellina gouldii prefers a sandy substrate within an association of sea grass in shallow water. Abbott (1958) has remarked that this species at Grand Cayman was found at depths between 6 and 25 feet in lagoons facing the open sea.

Range. From Bermuda, the Bahamas, Palm Beach, Florida in the north, this species extends through the Greater Antilles and Lesser Antilles to the north coast of South America.

Specimens examined. FLORIDA: off Palm Beach, in 100–130 fathoms (MCZ); off South Inlet, Lake Worth, in 7 fathoms (ANSP); off Miami, in 8–30 fathoms; off Fowey Light, in 25–38 fathoms; off Gov't Cut, in 5–35 fathoms; off Bear's Cut, in 18–20 fathoms; off Ajax Reef, in 4–40 fathoms; off Turtle Harbor, in 10 fathoms; Little Duck Key: off Conch Key, in 1–5 feet (all USNM); Tea Table Key (ANSP); Newfound Harbor Key; Key West; Garden Key, Tortugas (all USNM). MEXICO: *Albatross I* station 2365, 46 miles N of Cabo Catoche, Yucatan (22°18′ N; 87°04′ W), in 24 fathoms (USNM). BERMUDA: Castle Roads, Castle Harbor, in 4–5 fathoms; North Rock, 11 miles N of Hamilton, in 4 fathoms; Bailey's Bay, in 8 feet (all MCZ); Casper's Island (USNM); Shelly Bay (ANSP; MCZ). BAHAMA ISLANDS: off Gun Cay, in 9 fathoms (USNM); Dick's Point, Nassau, New Providence (MCZ); Mintie Bar, South Bight, Andros (USNM); Little San Salvador; Orange Creek, Cat Island; Simms, Long Island; Matthew Town, Great Inagua (all MCZ). CUBA: *Barrera* station 211, Cape Cajon; *Barrera* station 208, Bahia Honda, in 1–12 fathoms; *Barrera* station 206, off Arroyos; *Barrera* station 202, Cabanas Harbor, in 25 fathoms; Habana; *Barrera* station 201, Cayo Levisa (all USNM); Pueblo Nuevo, Matanzas; *Atlantis* station 2999, Bahia de Matanzas (23°10′ N; 81°29′ W), in 145–280 fathoms; Guarda la Vaca. Banes (all MCZ). HISPANIOLA. HAITI: Jerémié (USNM). VIRGIN ISLANDS: 1 mile E of East Point, Anegada Island, in 3–6 feet (ANSP); White Bay, Guana Island (MCZ); Judith's Fang, St. Croix (IMPBR). LESSER ANTILLES: Marigot Harbor, St. Lucia (MCZ); Carlisle Bay, Barbados, in 6–12 fathoms (USNM). CARIBBEAN ISLANDS: off Bowse Bluff and West Beach, Grand Cayman (both MCZ); SE of Swan Island, in 5 fathoms (MCZ). VENEZUELA: off Punta de Piedras, Isla de Margarita (ANSP).

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REPORT OF THE WORKING GROUP ON BIGEYE TUNA

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GEOGRAPHIC DISTRIBUTION

Unlike the skipjack and yellowfin tuna, the bigeye tuna is landed almost entirely by a single fishery, the Japanese longline fishery. This fishery is so extensive geographically, however, that it gives a good general reflection of the distribution of the resources. Data summarized by Rothschild (1966) showed catches in 1963 over the entire Pacific from Asia-Australia to the Americas, and from north of lat. 40° N. to south of lat. 40° S. This is substantiated by Blackburn (1965), who reports the range of the species to be from lat. 42° N. to 22° S.

The range of the bigeye tuna, like that of the other tunas, is related to temperature. The lower limit is believed to correspond to the 15° C. (59° F.) summer isotherm of surface temperature, the upper limit of temperature tolerance is unknown.

VERTICAL DISTRIBUTION

Here again the available information is chiefly from the longline fishery. Murphy and Shomura (1955) categorized research-vessel longline catches as ''shallow,'' ''intermediate,'' and ''deep,'' within a depth range of 200 to 600 feet. More bigeye tuna were caught on the deep hooks than on hooks at either of the other two categories of depth. A similar finding was reported by Shomura and Murphy (1955). More precise data were given by Yoshida (MS.)[1]. His results showed catches of bigeye tuna by 50-foot categories of hook depth. At ''oceanic'' stations catches were made at all depths from 200 to 549 feet, with modes at 300-349 and 500-549 feet. At ''insular'' stations the modal depth was 500-549 feet.

The extremely sparse data just given do not define the vertical distribution of bigeye tuna with precision. Most data indicate, however, that they occur somewhat deeper than the yellowfin tuna.

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[1] Yoshida, H. O. MS. Longline fishing for deep-swimming tunas in the Marquesas Islands and adjacent areas. Bureau of Commercial Fisheries Biological Laboratory, Honolulu, Hawaii.

SUBPOPULATIONS

Information on this subject is practically nonexistent. Morphometric data have not proved to have much utility. Preliminary work on blood groups by Fujino[2] has demonstrated two blood group systems which are amenable to Hardy-Weinberg analysis. It appears, therefore, that means for identification of subpopulations are available if effort is spent in that direction.

ESTIMATES OF BIOMASS AND YIELD

Preliminary assessments offered here have been obtained by assembling the rather sparse and rough data now at hand. Great caution should be exercised not to impute greater reliability to the estimates than they deserve. If more precise data are gathered in the future they may well lead to substantially different findings.

An estimate of possible maximum equilibrium yield has been produced by Silliman (1966). He obtained it by using a model with available data on mortality rate (annual mortality of 33 percent, or $Z = 0.4$), weight-at-age, and an assumed recruitment curve. From assumed values of annual natural mortality M of 18 percent, 14 percent, and 10 percent ($M = 0.20$, 0.15, and 0.10; $F = 0.20$, 0.25, and 0.30) catches were calculated for comparison with actual catches. Best agreement was obtained at an annual natural mortality of 10 percent ($M = 0.10$), for catches in 1944-61.

By adopting this value of natural mortality, equilibrium yields at several values of fishing mortality were calculated. Indicated maximum sustainable yield was 78,000 metric tons, at an annual fishing effort of 395 million hooks and an annual fishing rate of 45 percent ($F = 0.60$). Inasmuch as recent catches have been as high as 98,000 tons (1963), this estimate gives little encouragement for the expansion of yields by increasing fishing effort, with longline gear.

This pessimistic view of future yields tends to be substantiated by data summarized by Rothschild (1966). He showed an eastward expansion of the Japanese fishery from 1953 to 1963. From 1961 to 1963, however, declines were substantial in catch per unit effort in the eastern Pacific part of the fishery. Rothschild considered the possibility that this decline may have been caused by fishing. In such a circumstance, it is likely that fishing effort would decrease in the eastern Pacific, and increase in the central Pacific. Belief that the decline in CPUE (catch per unit of effort) may have been caused by fishing is supported by findings of Suda and Schaefer (1965), who demonstrated a negative relation between CPUE and fishing effort east of long. 130° W.

INFORMATION AND RESEARCH NEEDED

Limitations of the estimates reported above indicate that better data are needed as the basis of yield models. These data would include assessments of natural and fishing mortality rates, and production of improved curves of growth in weight. For the type of model reported above, the need is especially great for better knowledge of the stock-recruitment relation. Estimates of stock size can be obtained in any of the following four ways:

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[2] Personal communication.

1) Analysis of catch-effort data.

2) Measurement of larval abundance, including resolution of the problem of identifying larvae of bigeye tuna.

3) Tagging experiments.

4) Sonar surveys.

Verification of estimates should be attempted by using more than one approach. Measures of recruitment to relate to stock sizes may be secured from application of age analysis (as suitable) to the estimates of stock. Abundance of the first or first important age-group in the fishery may then be related to the size of the spawning stock that produced it.

It would also be useful to apply models which circumvent the requirement for detailed vital rates, such as the Schaefer approach.

Additional information on subpopulations is needed, and probably could be obtained from blood analysis.

Information on vertical distribution will be particularly valuable in designing effective fishing gear, both for research and for commercial production. Data could be obtained by one or more of the following:

1) Experimental longlining at a range of depths.

2) Attaching a depth recorder to existing longline gear.

In any event, vertical distribution should be related to oceanographic conditions, so that it may be generalized.

The abundance of small bigeye tuna, not landed by existing longline gear, should be investigated. Results should be referable to the problem of assessing possible increases in yield by reducing the age of entry into the commercial catch.

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The following symposium — Restoring the Quality of Our Environment: What Needs To Be Done and How We Are Doing It — took place at the North Carolina State University, Raleigh, N. C., during the 27th Annual Meeting of the Association of Southeastern Biologists, 14 April, 1966. The principal speaker was Dr. John L. Buckley, Office of the Science Advisor to the Secretary of the Interior. Discussants were: Dr. Theodore R. Rice, Director, Radioecology Laboratory, U. S. Fish and Wildlife Service, and Dr. Don W. Hayne, Professor of Experimental Statistics, North Carolina State University. The Moderator of the symposium was Dr. Arthur W. Cooper, Department of Botany and Forestry, North Carolina State University.

RESTORING THE QUALITY OF OUR ENVIRONMENT:

What Needs To Be Done and How We Are Doing It

John L. Buckley: Mr. Chancellor, Dr. Bennett, Dr. Cooper, ladies, and gentlemen — I should like to express my thanks to you all for the opportunity of being here this evening. I am not quite sure, from the diversity of the audience, what things I am expected to say. At the risk of boring some of you, it seems to me we need to talk a bit about organization and advisory mechanisms within the Federal Government. I recognize that organization can be a dull subject. Yet, if we don't understand the relationship of one group to another, I think the multiplicity of recent reports on environmental pollution is a little bewildering. Maybe it is bewildering anyway.

I don't have an appropriate joke about organization. The only one I can think of is this — and maybe it is appropriate because we are in a tobacco growing area. One of the cigarette advertisements of a few years gone by stressed "a thinking man's filter," and that reminded me of two friends, one of whom was a neural surgeon interested in the functions of the brain, the other was a sanitary engineer. These two men had spent a great deal of time fishing together over the years, and while they didn't have anything professional in common, they were very good friends through these fishing expeditions. Finally, the sanitary engineer, who ran the local sewage disposal plant, retired, and shortly after he retired he passed away. In his will he bequeathed his brain to his good friend, the neural surgeon. Upon hearing of this, the surgeon was delighted because he had always wanted to see "a filtering man's thinker." This kind of story is not very different from the semantic confusion which is present in many of our discussions relating to pollution. When we use the term *pollution,* it means many things to many people. When we use the word *environment,* it means many things to many people. As Dr. Cooper pointed out, I am now in the Department of the Interior, and when one says 'environment' in the Department of the Interior, it depends on who he speaks to as to what concept he elicits. To those people who are in the Geological Survey, for example, the word 'resources' brings to mind the non-living resources; the word 'environment' means to them really the atmosphere and the hydrosphere and the lithosphere. The Fish and Wildlife Service people, on the other hand, think first of living resources and their habitats. I think it's this latter view that most of us here are concerned with, the thin layer — the interface between water and air and land — which provides the basis for life as we know it. Such is the confusion of words.

One of the things that I intend to do, then, is to talk about what has led to the present interest in environment, and, more precisely, the pollution of the environment. It is not easy to point to any single event. To go back to 1961 and 1962, the National Academy of

Sciences — National Research Council put together a series of documents on natural resources. In these, they pointed out that one of the major problems facing the users of resources in the future would be pollution. Nobody paid too much attention to the comment at that time. There were some funds left over from that study, and the Academy put together another study group. It was concerned with environmental pollution, and recently, within the last month, in fact, it issued a document, "Waste Management and Control." This is a document well worth looking at. Something over a hundred people have participated in one way or another in its preparation, and it has a series of recommendations, some of which are novel and many of which are highly useful. In that same general period of time, within the Federal Government — to be specific, in the summer of 1964 — President Johnson was seeking to identify some of the most serious problems this Nation faces. In the process of doing this, some fourteen task forces were created to work for the President in different fields. One of these was the field environmental pollution, and a task force was established under the chairmanship of Dr. John Tukey, statistician and mathematician at Princeton. Most of the task forces of the Great Society ceased to exist after they finished their reports in early November of 1964. This particular one, however, continued on as a panel of the President's Science Advisory Committee, and produced the report "Restoring the Quality of our Environment," which was issued in November of last year. It is that report in particular, that I wish to talk about tonight.

What is the President's Science Advisory Committee, and where does it fit into the scheme of things? The President's Science Advisory Committee is made up of distinguished scientists appointed by the President, each of them for a four-year term. The elected Chairman of this group at the present time is Dr. Donald Hornig, a chemist. Dr. Hornig also is the President's Science Advisor by appointment from the President. He is Director of the Office of Science and Technology, which is a small group within the Executive Office of the President. He is also Chairman Ex-Officio of the Federal Council for Science and Technology, made up of the senior scientists from each of the larger departments of the government. Its membership is totally Federal employees. They offer advice to the President through Dr. Hornig. The other group, the President's Science Advisory Committee, is totally non-Federal. The members are all university or industry or non-Federal people. So the President has access to independent sources of advice on science matters.

There is no direct relationship between these organizations and the National Academy of Sciences. While I don't wish to belabor this point, it seemed to me important because a non-government group, the National Academy of Sciences, had identified deterioration of the environment as a major National problem, requiring some considerable understanding. The President intuitively identified this as an area he felt required considerable effort and understanding. The President's Science Advisory Committee had separately selected this as a topic worthy of study. Both of these groups, produced a report. The first of these, that by the Presidential task force, was presented directly to the President, with no copies made public. Parts of it did influence the legislative program, the budget of the United States, and were incorporated in the President's message on natural beauty which was transmitted to the Congress on February 8 of 1965. The second report, from the President's Science Advisory Committee, "Restoring the Quality of our Environment," was published with a strong letter from the President which ends by saying, "I am asking the appropriate departments and agencies to consider the recommendations and report to me on the ways in which we can move to cope with the problems cited in the report. Because of its general interest, I am releasing the report for publication." Within the Federal Government, when the President asks that an agency do something or another, it is pretty likely that the agency will do it. Consequently, there has been a considerable stir within the Federal Government as a result of this particular directive. It was backed up by a more specific directive from the Bureau of the Budget, which asked each agency to report specifically how it planned to react to the recommendations that had been made. It was not a directive to carry out all the recommendations, but it was a directive to think about the recommendations, and to consider how the problems can be solved. Several points stand out clearly in both these reports:

1. Pollution is a serious and growing problem, or more precisely a whole complex tangle of problems.
2. We can never eliminate pollution. We can and must find better ways to manage pollution at levels we can accept.
3. We can do a much better job of managing pollution with present knowledge than we are doing.
4. There is a great deal more that we need to learn before we can do an *adequate* job of managing pollution.

As biologists we recognize that pollution problems are not simple. You know more about many of the details of these pollution problems than I do, but I am impressed that not only biologists, but engineers recognize that biological understanding is one of the most pressing needs in pollution control. With this broader awareness will come increased funds.

The opportunities for biologists to contribute to maintaining environmental quality is most welcome. The greatest need that we can fill I think, is in providing the basis for environmental quality standards. Much of our work in the past has been concerned with demonstrating how bad a particular substance was. What we need to do, I think, is to learn what quantities of a substance or combination of substances can be permitted in the environment without causing damages that society is unwilling to accept.

The second point that I should like to make, is that we ought to employ biological foresight at the time that we make decisions affecting the environment. Sometimes we have done this and done it well. An outstanding case has been our management of radiation. Potentially radioactive wastes and by-products are among the most damaging substances to living materials. Perhaps because we were scared by the potential destruction of these materials, we approached their use with caution. The safeguards we have devised have made it possible to use nuclear energy with reasonable safety. We didn't have all the knowledge we would like to have had at the time we began to develop peaceful uses of nuclear energy. We don't have all the knowledge yet. But we did apply what we knew with the result that we will be able to reap the benefits of nuclear energy with a minimum of deteriment to our living environment.

At the other extreme has been our release of some toxic chemicals in the environment, with resulting effects which were apparently a surprise. It seems to me we can no longer afford the luxury of proceeding blindly. As more and more of us live in the same space, and as each of us generates greater quantities of waste, we shall have to provide a more formal mechanism to maintain the kind of environment we wish to live in. As a basis for providing this kind of environment we need a much greater understanding of the world in which we live.

Each of us here recognizes that we depend directly on many kinds of living things. Each of us here recognizes that these living things in turn depend upon other living things. Beyond our direct dependence for food we use some of these living things for recreating or esthetic proposes. But beyond these relatively obvious uses of other living organisms, there are some biological values and some services that are performed which are essential to the well-being of man. You all recognize the essential role of phyotosynthese in removal of carbon dioxide, release of oxygen, and conversion of incident energy. We exploit this process directly for the production of food. But we also benefit by the removal of carbon dioxide and the release of oxygen. How much must we affect the vegetation (including the marine phyto-plankton) of the earth to alter carbon dioxide or oxygen balance? Or we can consider the cycling of nutrients (or pollutants) that takes place in the waters and the land and the atmosphere around us. Here again, biological processes are important in breaking down, segregating and putting aside, eliminating some of these materials, rendering them into simpler forms. There are a whole series of services of this sort performed, and, again, we can't, I think, quantify the level of dependence that we have. For the most part it's more nearly an intuitive feeling that some of these services are indispensable to us than it is a definable quantified fact.

In terms of "what can we do about it," there are at least two general categories of waste products that we need to be concerned about. The first of these includes waste products that occur in concentrated form. Among these, I would include the municipal wastes, industrial wastes, the solid trash, and things of this sort that accumulate in cities. Clearly, we can't leave them in the places where they are; we must find some way of getting rid of them, and, in fact, we do, — through our sewer systems, dumps, incinerators, etc. There is another category of waste, which is in some ways more difficult to handle. These are the wastes that are by-products of some activity or another and that are widely dispersed. I would cite asbestos fibers that we find in sufficient concentration to occur in the lungs of people, or lead as we find in the atmosphere or plants, or soil, or water, which may have arisen from lead we have added to gasoline. There are a number of others.

The approach to control of these two types of wastes needs to be quite different. Considering the problem of deliberate waste disposal, we have followed a somewhat fragmented approach. We have people who specialize in this. We have other people in cities who worry about trash; we have others who worry about air pollution; and yet these things are not unrelated. They are very closely related. Somehow or other, we've got to find some way of incorporating a common concern in building the disposal of these into some unified system. I don't mean they have to be a single system. I simply mean we have to worry about optimizing over the whole range of disposal problems rather than within any one of these, as we so often have done in the past.

As to what we are doing about it, I touched briefly on this before, and I won't elaborate too much now, but there has been legislation passed in the last session of Congress in regard to water pollution, air pollution, and solid waste disposal. In water pollution, the Water Pollution Control Act was amended to require the states to submit standards of water quality for interstate waters, which after being accepted by the Secretary of Health, Education, and Welfare, would become established standards within that state. The deadline for submission of these is July 1 of 1967. Do we have enough information at hand to put together a reasonable set of standards? I am not at all sure that we do, but I wouldn't for a moment suggest that we delay establishing standards until we know all the things we'd like to know. I would rather move ahead and do the best we can at this time and consider whatever standards are established now as somewhat tentative in nature, subject to change as information is accumulated. I would also use the obligation to set standards as a strong weapon to increase the research that we now are carrying out.

Another action affecting water pollution is the Reorganization Plan that proposes to move the Federal Water Pollution Control Administration from the Health, Education, and Welfare Department to the Department of the Interior; the reorganization becomes effective sixty days from the time it is submitted to Congress unless the Congress disapproves. The waiting period on this is up on the 10th day of May of this year. To me, it seems quite likely that the Congress will not refuse the President on this and that the Federal Water Pollution Control Administration will be shifted to the Department of the Interior. There is concern about this reorganization among people who feel quite strongly that water problems are primarily associated with human health. They feel that if water pollution control responsibility is placed in the Department of the Interior, which is not really oriented to people's health, that Interior may let the rivers and streams get into a much worse condition than they are now. There is another group of people that feels that if you can protect the fish — they are much more sensitive than people — you automatically protect the people. This is the nature of the debate. It's not a very vigorous debate. Other actions that have been taken relate to solid waste. This is perhaps the least attractive field, and yet one of the more pressing problems that almost every community faces. There are only three or four cities in the United States, I think, that have a full time professional engineer who is responsible for the disposal of trash that originates within the city. More often than not, he is the guy who runs the highway department or something of this sort, who has a sideline to make sure that his trucks pick up the junk, and somehow or other get it out of the people's sight. This was all right so long as we had scattered communities. But now that we live closer together, I think this booklet on "Waste Management" here phrases it well. It says "one man's trash basket is another man's living space." In all seriousness, we are getting pretty close to this situation in some communities, so there are some difficulties here. The last session of the Congress did authorize a substantial program in the Department of Health, Education, and Welfare, within the Public Health Service, to stimulate work in finding new means of disposing of solid waste.

There are a number of other actions which are going on. Most of these relate to more and better than we have done before — more money, more research, more training of people. To this, I think we generally all agree, but not much of this relates to change in direction.

I think the main thing which causes the situation today in regard to pollution to be different from what it was three or four years ago is that there are groups such as this one you represent which are concerned, which look upon this as a problem, who can provide pieces of information that *do* fit in here, who feel that this *is not* beneath their dignity. These are definitely applied problems, things that we must find answers to. But in spite of being useful to mankind, they also have some fascinating, intellectually stimulating possibilities. Many of these have not yet been looked into, and most of them have not been pursued as far as they should be. I think there is considerable evidence that there is an increase in interest in this field, and there is certainly strong public support. Everybody knows about pollution now. In fact, it wouldn't be too difficult to see this awareness push actions further than it should — where people are scared when it's not necessary to be scared, where they demand expenditures that may be greater than we need. The question is 'how clean is clean?' How clean *can we afford* to have rivers? How clean *must we have* rivers? In many states, for example, the Conservation Department may have certain responsibilities in regard to water pollution. It may, for example, be almost the sole arbiter as to the cause of the fish deaths; yet have no enforcement responsibility. And what this amounts to is power of influencing the public — power without responsibility. It seems to me that we could overplay this business of how bad pollution is. We could overplay on how much we should spend and how clean we must have our surroundings. I don't think that we will, but I think the only way to assure that we don't and to assure that we *do* make expenditures that we must make and that we *do* have things as clean as we need to have them will be on the basis of information, much of which has not yet been gathered. I rambled on much longer than I should have and I'd like now to turn this over to Dr. Cooper; and if the opportunity permits later, I will be glad to evade or answer questions, as the case may be.

Thank you.

T. R. Rice: Mr. Chancellor, President Bennett, and ladies and gentlemen. — As we learned from Dr. Buckley's interesting and informative talk, to improve the quality of our environment will require the cooperation of all and the integration of political, scientific, and social aspects of the problem. Also, it must be obvious that a much greater expenditure of money than now goes to this problem will be needed to correct the rapidly deteriorating condition of our environment and to maintain it in an improved state. Twenty or 30 years ago most people would have been amazed if told that highways would eventually cost a million dollars per mile. Yet today we have thousands of miles of highways costing this much, or even more. We should not, however, approach the problem of improving the quality of our environment as we did in the building of our roads, advancing from dirt and winding roads to modern four-lane interstate highways. In our improvements we should look ahead and build and work with sufficient foresight that we will not have outgrown our improvements by the time we obtain them.

If we are to build intelligently for the future we must first answer the question, "What type of environment do we want"? Those with the pristine view would not permit any pollution of our environment, while those with the sterile view would permit an unlimited amount of pollution. It is obvious that we cannot follow either of these courses. Rather, if man is to consider himself ecologically a part of the environment and take an ideal approach, he must consider all effects of pollution of the environment. Even with this logical approach, we will, no doubt, be faced with many difficult decisions.

In our search for the best and most expeditious ways of improving our environment we will make many mistakes, but let us hope that we shall be as fortunate as we were in establishing our government. We often have heard it said that, although our democratic form of government is not perfect, it is the best government in existence today. Similarly, we can say that thus far we have had no perfect plan for disposal of any waste, but we believe the disposal of radioactive materials is an example of a well-planned system. Injury and loss of life from disposal of radioactive materials or from accidents involving these materials have been minimal. Now let us consider why.

1. The public, legislators, and scientists must be aware of the dangers associated with a problem before it can receive sufficient financial support. The atomic bomb very effectively acquainted the public with the dangers of radioactive substances. Although the improvement of the quality of our environment will require the cooperation of the present generation, we must also obtain the support of future generations, since the improvements must be maintained and possibly broadened. Thus, to prevent people from becoming litter bugs, polluters, and destroyers of our environment, I advocate more emphasis, starting with the first year of school, on nature study and establishing an understanding of the importance of the environment to man. This indoctrination is important if the vital role of the environment in man's welfare is to be placed in proper perspective.

2. *Research* to develop the atomic bomb was supported on a national basis. The bomb was born in secrecy, yet the potential danger of radiation to man has grown since 1896 when the existence of radioactive elements was discovered by Becquerel. Research to protect man against radiation effects and levels of radioactive materials that could be released progressed with research on the bomb. Similarly, there should be no significant disposal of any waste material until its effect on man is known.

3. From this research came *standards* for the handling, shipping, and disposal of radioactive substances. Standards for radioactivity are contained in publications such as: Standards for Protection against Radiation, Title 10, Part 20, U. S. Atomic Energy Commission; Reports of the National Committee on Radiation Protection; and the International Committee on Radiation Protection. Standards for any waste disposal should be for the entire United States, as they are for radioactivity. No one should be penalized because of his geographical location. In contrast, however, the numbers of *E. coli* that can exist in a body of water before it is considered polluted now varies among the states.

4. After standards and guidelines were established, an extensive *monitoring system* was inaugurated and has been functioning for years. The atmospheric, aquatic, and terrestrial environments were sampled frequently and on a broad geographical basis.

Man can modify his environment both in beneficial and in deleterious ways. I have referred mostly to how man injures his environment by releasing wastes into it and have emphasized the need for examining the total effect of these substances upon different forms of life. The effect of a given substance upon an organism can vary with the amount of substance present. Pesticides began to be used in relatively large amounts just after World War II, but it was not until 1962 when Rachel Carson's *Silent Spring* was published that more nearly adequate amounts of money became available for research into the effects of these materials.

In addition to more research into the deleterious effects of waste materials upon the environment, more consideration should be given to the use of waste materials for beneficial purposes. Great emphasis has been given to finding "Peaceful Uses for Radioisotopes" as indicated by a number of international meetings on this subject. As we all know, the use of radioisotopes has had a tremendous impact on research, medical practice, and certain areas of industry.

There are other instances of practical uses of waste materials. The common aspirin originated years ago from a waste material, acetylsalicylic acid, through the ingenuity of a researcher of the I. G. Farben Chemical Company in Germany. Also, stickwater or wash water in a menhaden plant which a few years ago created a waste-disposal problem is now mixed with fish meal, passed through the dryer, and effectively incorporated into the meal.

I would not want anyone to conclude that we have all the answers concerning radioactive waste disposal and the levels of radiation to which man can be exposed. Based on research findings, the maximum permissible concentrations to which man can be exposed are continually being examined and changed. For instance, two areas requiring more research are the effects of low levels of radioactivity over long periods of time and the effects of various mixtures of radioisotopes. In general, toxicity studies on any substance usually involve concentrations which result in the death of 50 percent of the test animals in a relatively short period of time. Yet, man is exposed in the natural environment to lower levels of many toxic materials over a lifetime. Also, one needs to consider whether tests relating to exposure to a single substance have any real significance. Threshold-limit values now have been accepted and are being applied to industry for some 300 waste materials. Of these values, probably not more than 10 have been studied sufficiently to ensure levels which would result in a safe and healthful environment over a full working lifetime. If the substances were mixed together, what would we know about their effect?

Advances are being made in other areas which will contribute also to restoring the quality of our environment. Control of the population explosion will contribute, since waste disposal is directly related to the total number of people and to their standard of living. Modification of the weather has been attempted without much success in the past, but it is expected that in the next few decades it will be possible to increase precipitation in certain areas. Water used for cooling in industrial processes is presently suitable for re-use and by the year 2000, the volume required for cooling may exceed all other uses of water combined. We therefore must make plans for handling this large demand for water before the need arises. Research into this problem is now progressing satisfactorily.

The level of contaminants in water must be controlled because we will be faced with an ever-growing demand for water. The ways in which water is used and re-used and is renovated and conserved, no doubt, will be changed through research by the government, industry, and universities. Although technology will dictate to a certain extent many future uses and re-uses of water, public regulation and economics also will influence our use of water resources.

Dr. Don. W. Hayne: Chancellor Caldwell, Dr. Buckley, Dr. Bennett, ladies and gentlemen. It is a real and personal pleasure for me to be here for I have been associated with Dr. Buckley in different capacities for years. Curiously enough, it happens that I have not before heard him give a formal lecture. Many times I have heard him talk to his staff as a really superlative administrator of a research center, and later I saw him in action as an effective staff man of a panel. Now this, the first formal lecture, comes up to the other standards.

I am going to comment briefly as what we might call a technician in this area, speaking mostly to other professional biologists who may be ready to consider for the moment the view of a technician. I wish to mention a few problems of ecologists who accept the facts that, as Dr. Buckley has pointed out, there is here both a broad interest and a need for the work. As Dr. Rice has pointed out, we need money, but when we have this degree of interest at the national level the money is there. In fact, it is my impression that we have more money than good work to be supported by it.

As biologists, we have talked about this pollution problem for so many years that it is now almost automatic. But at last we are faced with the fact that we must now produce something more than talk. What are we going to do? This is a very tough problem which I cannot solve tonight, but I want to talk about a few of its phases. First, our interests are really greatest regarding the effects at the lower levels of exposure. Dr. Rice touched on this problem. True, we are horrified by those disasters which occur from unwise and unwarranted use of pesticides, or from the occasional accidents with isotopes or reactors, but these are not the things which the biologists in his professional capacity is going to be called upon to worry about. These high level effects are apparent to everyone and they are being taken care of, as we have been told. Our problem is how we are to deal with this problem of detecting the effects on the biota, the environment and the whole ecosystem, of exposure at low levels.

If we must talk in terms of life-time effects, then how are we going to work with these problems, for they are literally those of a life-time? I do not have the answer, but I think that this general problem is going to challenge us, as biologists, and as experimentalists to devise methods of working with it. This problem is not new, of course, it is exactly the same question faced by medical science in working with carcinogens, or with any suspected toxin. Here you must define a substance as not to be tolerated at some level far below that where it will produce any appreciable and measurable effect under experimental conditions. For our part we are now concerned with the effect on our environment of pollutants, and, as I said, we must truly be concerned professionally with the low level effects, not with the intermediate and obvious effects, but the subtle effects, the long-term effects. We hear emotion talk of banning use of every chemical which is toxic at any modest level, but I believe that rather than accept this costly concept, we must learn to appraise the low-level effects.

As a second point, the effect of environmental contamination on natural populations is a promising tool as well as an interesting and challenging problem. I wish to comment on one possible parameter for study, and the implications of considering this. For some time now ecologists have been concerned with the structure of a community, that is, number of species present, number of individuals per species, the kinds of species, whether there is a pattern in the occurrence together of a series of species, why the pattern occurs as it does, and what will change it. It is apparent that pollutants change this pattern or structure of the commumty. Certain species are benefited, or at least they increase in numbers and by the rules of the game we say they are benefited. Other species decrease or are eliminated. Up to now, we have worked on this problem largely in a non-quantitative sense, and it is clear that we must now move into a much deeper understanding and a much more use of this concept for studying environmental changes. And, yet, the people who wish to study environmental changes usually are not the same people competent to handle the genuine and vexing taxonomic problems involved here. So, in such studies we have been handicapped by the fact that if you wish to work with a community, a natural population of species, you must somehow combine a taxonomic ability with the aptitudes of the population ecologists, and some competence in mathematics. Since the first characteristic is so rarely associated with the others, it seems to me to follow that one of needs growing out of our concern with pollution these days is a very much increased support for the taxonomic sciences, and some means of making services of this group more readily available. Working taxonomists are overworked now in their attempts to help others. We need a better way for providing their services to the practicing ecologists in some organized manner which will allow the studies of both to flourish.

With the lateness of the hour and the thorough coverage presented here by others I will conclude my remarks here. Thank you.

Audience Participation

Jesse C. Thompson, Jr., (Hampden Sydney College): Dr. Buckley, your remarks are very much different from those of Dr. Egler, our speaker at the symposium last year. You seem to be more subdued in your discussion of this important problem and, if I understand correctly, you are saying that all is going well and that the Great Society is taking care of everything. You even stated that possibly we may even be getting too concerned about the pollution of our environment. Do you believe there is more danger in being too concerned or too little concerned?

Buckley: Let me try to show you what I meant -- I am sorry I didn't jump up and down on the platform. It isn't that I am less concerned than was Dr. Egler. It seems to me that what I was trying to say in this particular context, and I am glad you raised the question here, is that *the burden is on us to make sure that the dollars spent buy the things that we want bought.* I can foresee large expenditures for sewer systems and the hardware for sewage treatment plants, and similar sorts of thing. All I am suggesting is that we make sure that when we spend that money it buys the kind of control that we want bought. If we are not prepared to use wisely the funds provided by the public, I am worried more about an embarrassment of riches rather than the other way around. There was $120,000,000 of money this year (the 1967 budget) that wasn't in the 1966 budget. And this year almost every other kind of program, except the war in Viet Nam, was cut. So I am trying to point out that money is available. There is public concern. We don't know all the answers we want to know. I would prefer to go slow on those kinds of things where we are not quite sure. I would like to be as vigorous as possible in cleaning up where we know how. Shouting that this river has got to be clean as it can possibly be, or that we can't afford a speck of dust or sulfur dioxide in the air — I don't think this is what's going to get us places. We have to look at it the other way around. There will be sulfur dioxide; there will be dust particles; but there need not be the quantities that there now are. I was recently in Germany, I can't vouch for the validity of these statistics, but they were given us. They are that on the average in industrial cities in Germany there are 85,000 particles of dust in a liter of air. In forested parts of Germany, there are something like a hundred particles to the liter of air. The point I am trying to make is that there is room for improvement in every industrialized country. Another point connected with this, it seems to me, is the matter of who pays the bill. And it seems to me that one of the pronouncements made in this "Restoring the Quality of our Environment," and since made by President Johnson, has been that there ought not to be, that there is no right, to pollute; that, rather, industrialists must begin to consider, as a cost of doing business, the proper disposal of the waste products that result from their manufacturing processes. Now, you couldn't have said this five years ago, but this is a statement which is generally believed by the American public today. I think that Federal expenditures will be related to cleaning up what's already happened; to restoring those things that have already been deteriorated; but the cost of prevention of further pollution ought clearly to be borne by those people, those industries, those municipalities that would otherwise cause this pollution.

Winston Menzel (Florida State University): I think this pollution problem is ironical. The biologists of my acquaintance have been aware of the evils of pollution problem for a long time, but, it took Miss Carson to explode the atomic bomb. I am glad she did. Dr. Rice said that radioactivity has the best control. That is true. We know the dangers of it. There has been more money spent on radioactive control — and more research. So my plea is to spend more money, even though we do make mistakes. We certainly spend enough on radioactivity control, and there have been more people killed, or harmed from pollution, than from any radioactivity.

Buckley: Maybe I need to draw the line in a different place. Most of us in the room are interested in this problem from the point of view of science; and yet, the cost of research associated with this sort of thing, I look upon as being fairly small. We are talking about a relatively few millions of dollars, 50 or 150 — something of this sort. What costs money is the "hardware" for control and treatment. Let me give an example. One of the ways that one can possibly solve the problem of combined sanitary waste and storm drainage is to build two separate systems, two sets of pipes; but if we were to do this in the older cities of the United States, the estimates run at something like $20,000,000,000. Now, are there other ways that we can solve that problem? Secondly, it's not at all clear to me, on the basis of what evidence I have seen, that with two sets of pipes we still won't have a problem bigger than we wish to have. The evidence I have seen strongly suggests that the surface drainage that comes from the city itself causes a sufficient oxygen sag and carries a sufficient quantity of materials picked up from the roadways, and so on, to be in its own right detrimental to the waters. And, yet, we have serious proposals to get on with this business of tearing up all the streets of all the major cities, laying two sets of pipes instead of one, and solving the problem this way. This is the kind of thing I am talking about as perhaps an ill-advised expenditure. Maybe this is the only solution — and if it is, then these are costs we ought to be prepared to bear. On the other hand, if we are talking about more money for research, then I agree with you. We have spent too little — we need to multiply our expenditure over the next several years. I are not suggesting to the contrary. I hope this makes people a little more comfortable. I don't intend to sound complacent.

Leon Hicks (Loyola University, New Orleans): I have a question of Dr. Rice. I believe you said, concerning the advances in the disposal of Radioactive waste, that we could probably apply these advances to other waste disposals. I saw pictures of the incident of the hydrogen bomb over the Spanish coast where there were barrels of radioactive dirt that were going to be disposed by just dropping them into the deepest parts of the sea, in radioactive dumps, and I have heard that waste materials from reactors are disposed of in that manner. I'd like to know, is that the advances in radioactive waste disposal that you were talking about? It seems to be parallel to dumping garbage outside the edge of a town, and since there is a foreseeable increase in reactor applications, are there going to be any advances made in this wholesale junking of radioactive waste?

Rice: My comments that what we had learned in the disposal of radioactivity could be applied to other wastes, of course, had reference to generalities; the same thinking, the same general approaches and research, financing, publicity and other things could be applied to any waste; and I would like to make a comment on your disposal. Most of you probably know that radioactivity is different from any other type of waste. Most wastes, with time, are degraded biologically or otherwise. But there is no way of changing the rate of decay of radioactivity. Only time can eliminate it. Therefore, there are two ways of handling waste. One is to contain it, to put it somewhere that it will be of no danger to anyone — and this is often done by putting it into deep wells; the possibility of storing it in salt domes in some of the southern states, or putting it in the depths of the oceans. Theoretically, I should mention, in these cases it is contained in thick containers that sink to the bottom and remain intact, and by the time it has disintegrated the radioactivity will have gone. The length of time required for the water from the depths to be circulated back to the surface is of such a magnitude that there would be no danger from long-life radioactivity placed in the depths. The thinking has changed somewhat in recent times, and there is no longer this wholesale disposal in the ocean. We do not like to think that the ocean is a garbage pail, but man has looked to some parts of his environment as a means of disposing unwanted material, and the ocean, being so deep, he naturally has taken advantage of this, and still does today. Well, I should mention that there is another way of disposing of radioactivity also, and that is to dilute it in such a concentration that the total volume of our breath, the total amount of water that you drink, or the food that you eat, would never contain sufficient radioactivity of accumulating sufficient activity that you would suffer any harmful effects. Now, we are sort of fixed — if we can have "X" amount of radioactivity in a liter of air and there are so many liters, once we have reached this threshold we must contain the radioactivity. So while we may use an intelligent approach to disposal of radioactivity, we still are faced with the problem. Shall we keep it all hidden, or shall we release some of it? And we feel that some of it must be released, but not in an uncontrollable amount.

Frank McCormick (University of North Carolina): I'd like to address my question to Dr. Buckley. It seems that we have mostly discussed how we might modify the results of a problem rather than how we might fight the problem itself. I think the President and most of the agencies of his Great Society Program recognize the problem; the problem being that pollution increases primarily because there are more people — the more people, the more pollution. Wouldn't it be more feasible to attack the problem of population control?

Buckley: I guess I will label that a political question rather than a scientific one and refuse to answer it. Seriously, I think your statement is essentially half true and half untrue. It seems to me there are two things that are happening at the same time. There is an increase in population; no doubt about this. But even without this increase in population, there is an increasing use of resources and an increasing volume of waste generated by each individual. What I am saying is that pollution increases at a faster rate than the population. Certainly population reduction would be one of the ways of reducing it, but on the other hand, it is not likely to be a very rapid procedure. If we were able to reduce the *rate of increase* of population in the United States or the world in the very near future, we still would end up with a population very much larger than it is now and still be faced with a need to do something to better the condition of the environment we now live in.

I would also point out that there are other things one can do about some kinds of pollution. You can use other sorts of materials, which create less of a pollution problem. Perhaps we can find other means of powering automobiles, for example, which would not have all the noxious by-products. Who is going to push this kind of thing? How do you move it from the idea that it would be nice if we did this, to something that you can go into the marketplace and buy? I don't think we have found any way of doing this yet.

One other point I intended to make before, and I will volunteer now. We were talking about ecology a good deal. One of the points in relation to ecology, it seems to me, is that there isn't a central place in the Government where one can put his finger on what we do know.

Many of you people know locally what a community looks like, what it's made up of, and what's happening to it, but at the same time there isn't any centralized place where you can begin to piece together a picture for the country as a whole.

Ecology is a field where almost every agency in Government has some concern — and each agency considers it is doing most of the things that need to be done in its area of responsibility. Yet it seems that there is a need for some additional work, particularly work done in the universities — basic research in ecology, better understanding of ecosystems, better understanding of population ecology. Much of this doesn't have an immediate practical application; yet, some of the things that Dr. Hayne said reminded me of this. He talked about changes in community structure — and I would ask you, changes compared to what? There are very few communities that we know enough about to measure whether, in fact, a change is taking place or not. If you ask a man who is working in pollution how he knows that a particular piece of water is polluted, pin him down hard, at last you find out that a piece of water is polluted *because somebody says* it is polluted. It may be a governor, a group of local citizens, but somebody has decided it is polluted. There doesn't seem to be any uniform basis on which you judge pollution. And, here again, research aimed at understanding what takes place without pollution, or with a minimum of pollution, seems to me one of the things we most need. There is a certain amount of concern in the Congress in relation to this. There are some bills, one of them introduced by Senator Nelson, which propose some increased activity in the field of ecology. Hearings are scheduled for the latter part of this month. Legislation of this sort ought to be of interest to you people in the universities. You ought to be looking for monies to begin to fill some of these needs.

William D. Burbanck (Emory University): I wonder, in this age when we get all our daily vitamins in one cereal at breakfast, and when we will not buy an apple having a wormhole, or an oyster with an imperfect shell — whether there is any way that we might begin to educate ourselves to the point where we don't need quite so much perfection in everything? It seems to me we have become almost ridiculous in our demands. If we cut down on our demand for perfection a little, perhaps our suppliers could cut down, and we could then get some sort of equilibrium.

Rice: Regardless of how concentrated man produces his vitamins or any other essential food ingredients, he still requires a certain amount of bulk. Years ago I heard some discussion that in Germany they were beginning to add essential ingredients to sawdust, and that this would make a very appetizing and nutritious food. But we are going to have to continue to eat a certain amount of raw material. So we are going to have to produce it. The question is, can we sacrifice, as Dr. Burbanck mentioned, the appearance of an apple, and have just as many apples per tree, or do we want more apples per tree, and, as a consequence, more pesticides in the environment? Of course, we come back to the population problem again. We have so many acres of land, and it has been estimated by the year 2,000 if we continue to increase at the present rate there will be one square yard of land per person. We must have so much food for the present and for future populations. Thus, we must grow more food per acre. We not only will have to use more pesticides, but also more fertilizers, and we can — when we hear there are certain pesticides in certain foods — boycott them. But, I do not know a simple answer to your question.

Buckley: May I add just one more comment here? I think this question and this response sort of pointed up the nature of the pollution question. There are separate actions we can take. But the problems cut across almost everything that we do, and we aren't going to sit in a room and solve all the problems. We will solve them back in our respective laboratories and not here. If we recognize they exist, if we tell the public they exist, if we help educate people, then we have begun to get some handles on control of pollution. Right now we have stirred the public up to the point they want to do something. It seems to me that we need to tell them what it is that they need to do. Before we can tell them some of the things they need to do, we need to find out ourselves. I hope you all go home and apply for grants from wherever you think you can get them; that you will all turn your interest to solving some of these fascinating problems that exist in pollution. By the time you treat the subject at next year's meeting, you will all be personally deeply involved.

Margaret Menzel (Florida State University): I'd like to address a question to Dr. Buckley. It seemed to me he indicated several times that really the crux of the problem is social and not strictly biological or scientific and he has indicated areas, such as city planning, control of human reproduction, and some other problems in human psychology, which would be basic to a solution. I'd like to ask him what amount of money is devoted to in research in these areas compared to that devoted to remedying the effects of the problem?

Buckley: I can't give you any fixed answer. Social aspects are very important — the attitudes of people, pressures in city planning, the overlapping of jurisdictions. I am thinking of the Lower Delaware Valley area, for example, where there are three states, eleven counties, 377 communities, 4,000 civic organizations, all wound up in one area that uses the same water supply and disposes of its waste in the same place, and yet each may have a somewhat different interest in how this water is used. How do you operate in a system such as this? I singled that out because we happened to have some numbers. But you can look at other cities. You can go to California — take Los Angeles County — and within the county you find other communities. These are very real problems, and they are ones we must find a way to handle. At the same time, there is another kind of problem that I don't feel we know enough about. Somebody has referred to the earth as a spaceship, a self-contained environment. We aren't going to add anything or get rid of anything that's on it. Our choices in disposal of waste become those of segregating it in some fashion and storing it away or returning it to the environment in such a fashion that it isn't harmful. Basically, these are our choices. We have got to learn to re-cycle, to re-use. These, too, involve social problems. How do you make people in a large city take water they know has already passed through the city and has come from the sewage treatment plant and to the water treatment plant and is re-cycled? This has been done in a few places where drought has been extremely severe, but it's a pretty difficult problem to make the people of a community believe that this is the best they can get. In fact, it may be purer than water they now use. It may be chemically and biologically suitable, but you can't get away with this without some degree of education in the community. I can think of at least as many social problems as there are biological ones. I am sorry I didn't emphasize this before because certainly it's severe and a real part of the problem which has not received the type support which it should.

C. REPORT ON THE INVESTIGATIONS BY THE UNITED STATES FOR THE INTERNATIONAL NORTH PACIFIC FISHERIES COMMISSION—1964

U.S. Bureau of Commercial Fisheries
Biological Laboratory, Seattle, Washington
February 18, 1965

INTRODUCTION

The bases for research activities of the Seattle Biological Laboratory were broadened in 1964. Our efforts in the past were directed rather intensively to defining the oceanic distribution of Asian and North American salmon as required by the Protocol. Some of these activities have been continued, but within the context of the broader problem of understanding the factors regulating the success of salmon populations at sea. This new perspective has resulted in some changes in the direction and emphasis of our research. Studies of population dynamics and ocean growth and mortality were initiated. Methods of identifying the racial origin of salmon using scale characters have been sufficiently developed, so morphological studies have been discontinued and superseded by scale studies. The king crab studies have also been phased out. This report describes the progress made in all programs during 1964.

TAGGING STUDIES

by A. C. Hartt, M. B. Dell
and S. B. Mathews

Tagging by the United States in 1964 was performed by the Fisheries Research Institute, College of Fisheries, University of Washington, under contract to the U.S. Fish and Wildlife Service, Bureau of Commercial Fisheries. Separate tagging conducted by the Bureau of Commercial Fisheries in growth and mortality studies is reported in the section entitled " Ocean Mortality and Growth ".

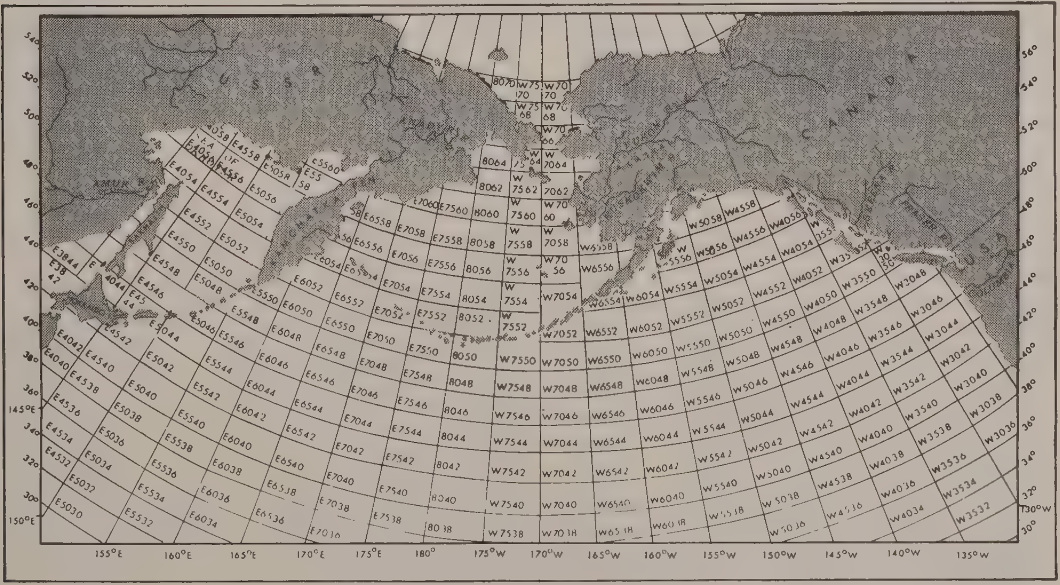

FIGURE 1. INPFC North Pacific area coding as modified for tagging.

Winter Tagging

Fisheries Research Institute personnel tagged some of the salmon taken during an exploratory fishing cruise aboard the Bureau of Commercial Fisheries research vessel *George B. Kelez* from January 17 through March 18, 1964. Station locations and catches are reported by the Bureau of Commercial Fisheries in detail in the section entitled " Salmon Distribution and Abundance ". The cruise track extended in a zigzag pattern across the central Gulf of Alaska, south of the eastern Aleutians, and in the Bering Sea between longitudes 175°E and 180° northward to 57°N. Longlines were the principal gear used to capture the fish. A total of 170 salmon (134 sockeye, 21 pink and 15 steelhead) was tagged. This preliminary work was helpful in suggesting ways of improving methods and gear for winter salmon tagging. Two sockeye tags have been returned as described in the section on tag returns.

Spring and Summer Tagging

In the three areas of operation, the main objectives were as follows: (1) In the Gulf of Alaska—to fish and tag over wide areas for comparison of distribution, abundance, migrations, timing and sizes of all species and age groups with those of previous years for use in future forecasting. (2) In the central Aleutian area—to obtain an index of abundance and

Table 1. Numbers of salmon caught and numbers tagged in spring and summer *longline* operations by U. S. tagging vessels in 1964.

Area[1]	Inclusive dates	No. of longline sets[2]	Number caught (tagged)						
			Sockeye	Chum	Pink	Coho	Chinook	Steelhead	Total
8050	6/8-7/10	3	28(26)	35(33)	50(42)	3(2)	5(3)	—	121(106)
W7052	6/6	1	87(71)	45(28)	7(3)	—	—	—	139(102)
W6552	6/5	1	18(18)	11(11)	2(1)	—	—	—	31(30)
W6054	6/4	1	38(36)	25(20)	3(3)	—	—	—	66(59)
W5556	5/30-7/13	5	28(24)	67(44)	158(119)	5(1)	—	1(1)	259(189)
W5554	5/15-7/14	5	65(59)	78(63)	17(12)	1(1)	—	6(4)	167(139)
W5552	5/14-5/28	3	102(93)	20(17)	4(4)	—	—	—	126(114)
W5550	5/21-5/27	2	140(123)	8(8)	25(18)	—	—	—	173(149)
W5548	6/23-6/26	2	95(80)	20(18)	44(37)	—	—	3(2)	162(137)
W5546	6/24-6/25	2	41(39)	6(5)	12(10)	—	—	4(4)	63(58)
W5056	6/19-7/10	6	97(84)	66(59)	135(119)	9(7)	—	1(1)	308(270)
W5054	5/14-7/15	8	537(433)	158(125)	192(150)	3(3)	1(—)	6(3)	897(714)
W5052	5/13-5/28	2	144(131)	5(5)	4(4)	—	—	—	153(140)
W5050	5/10	1	46(45)	7(7)	—	—	—	—	53(52)
W5048	5/9-5/26	2	184(147)	5(2)	28(26)	2(2)	—	4(4)	223(181)
W5046	5/25	1	1(1)	8(7)	50(38)	3(3)	—	1(1)	63(50)
W4558	8/26	1	—	3(2)	—	—	—	1(—)	4(2)
W4556	6/16-7/9	4	91(68)	145(103)	249(172)	15(11)	—	1(—)	501(354)
W4554	5/13-7/17	8	422(349)	46(36)	617(406)	17(9)	1(—)	5(2)	1,108(802)
W4552	5/10-5/21	2	127(116)	16(15)	2(2)	—	—	—	145(133)
W4550	5/8-5/22	3	179(132)	24(22)	33(18)	2(2)	—	2(2)	240(176)
W4548	5/7-5/23	3	301(202)	55(45)	35(25)	4(3)	—	6(5)	401(280)
W4546	5/24	1	1(1)	12(8)	81(61)	7(6)	—	3(3)	104(79)
W4056	6/11-7/22	6	27(22)	6(3)	420(322)	37(13)	—	—	490(360)
W4054	6/8-7/19	5	107(83)	84(56)	766(620)	19(7)	—	2(—)	978(766)
W4052	7/23	1	9(8)	—	32(24)	—	—	1(—)	42(32)
W4050	5/7-7/24	2	13(12)	1(1)	2(2)	—	—	1(1)	17(16)
W4048	5/6	1	43(37)	18(17)	8(5)	—	1(1)	1(1)	71(61)
W3554	6/10	1	7(5)	—	24(22)	11(9)	—	—	42(36)
W3550	5/6	1	11(6)	2(2)	13(10)	—	—	—	26(18)
W3548	7/25	1	—	—	—	—	—	—	—
W3048	5/2	2	—	4(3)	11(10)	—	1(1)	—	16(14)
Totals	5/2-8/26	87	2,989(2,451)	980(765)	3,024(2,285)	138(79)	9(5)	49(34)	7,189(5,619)

[1] See Figure 1.

[2] All were dawn sets; most sets were 20 skates of gear.

age composition of immature sockeye salmon south of Adak for use in forecasting the 1965 Bristol Bay run. (3) In the northeastern Gulf of Alaska—to study the distribution, abundance, migrations, and sizes of all species of juvenile salmon in their first summer at sea. The northeastern Gulf was chosen for this work to utilize data from current studies of fingerling salmon by the Bureau of Commercial Fisheries in Icy Strait, lower Chatham Strait, and Sumner Strait, and to extend these observations farther seaward.

Secondary objectives were: (1) To test a snap-gangen type surface longline in comparison with the standard Japanese longline. (2) To experiment with sonic tags as a means of following the movements of individual salmon at sea. (3) To test longlines with small hooks and baits for taking small salmon in their first summer at sea. (4) To test dart tags and to develop methods of handling and tagging fingerling salmon during their first summer at sea.

Vessels, Gear and Itineraries

The purse seiners *Commander* (81 feet) and *Storm* (81 feet) were chartered for the 1964 tagging work. Both vessels left Seattle on April 29. The *Storm* returned on September 1, the *Commander* on September 25. Both vessels carried Japanese-type surface longlines and fine-meshed purse seines identical to those used in 1963 (400 x 25 fathoms).

Operations in the Gulf of Alaska

Objectives were satisfactorily achieved, considering the extent of area covered by the vessels and the use of only one vessel after June 1. Longlines were used principally and seines very little. From April 30 through June 1, both vessels fished a series of stations between Cape Flattery and Kodiak Island and from 47°N to 57°N in the central and western Gulf. On June 1, the *Storm* proceeded to the Adak area. The *Commander* remained in the Gulf from June 1 through July 21, repeatedly fishing a series of stations spaced 2½ degrees of longitude along 55°N and 57°30′N latitudes between Kodiak and Sitka.

Longline catches are summarized by statistical area in Table 1. Some observations from the Gulf longlining operation are presented.

(1) Pink salmon catches were greatest south of 50°N during early May and increased northward and northwestward as the season progressed. Coverage was not sufficient to show the southern limits of their range. By mid-June, pink salmon were abundant in catches as far north as 55°N and were concentrated largely in the eastern half of the Gulf. In early July,

TABLE 2. Numbers of salmon caught and numbers tagged in spring and summer *purse seine* operations by U. S. tagging vessels in 1964.

Area[1]	Inclusive dates	No. of purse seine sets	Number caught (tagged)						
			Sockeye	Chum	Pink	Coho	Chinook	Steelhead	Total
8050	6/15–8/15	65	5,733(4,039)	6,809(2,854)	261(255)	6(4)	29(17)	—	12,838(7,169)
W7552	6/14	3	—	7(7)	2(2)	—	6(3)	—	15(12)
W5550	5/27	1	3(3)	—	—	—	1(—)	—	4(3)
W5054	5/29	1	15(15)	3(3)	—	—	—	—	18(18)
W5052	5/28	2	8(7)	3(3)	1(1)	—	—	—	12(11)
W5050	5/27	4	67(59)	3(3)	4(4)	—	—	—	74(66)
W5048	5/26	3	59(47)	3(3)	20(13)	—	—	2(2)	84(65)
W4554	7/17	1	3(3)	27(22)	17(14)	1(1)	—	2(2)	50(42)
W4546	5/24	2	2(2)	8(8)	23(22)	—	—	2(2)	35(34)
W4058	8/14–9/11	7	220(51)	167(26)	1,869(281)	236(51)	2(1)	—	2,494(410)
W4056	8/10–9/7	15	1,373(401)	524(115)	3,568(858)	388(162)	6(1)	1(—)	5,860(1,537)
W3556	8/22–9/19	4	12(—)	3(1)	15(7)	5(1)	2(2)	—	37(11)
W3554	8/7–9/20	8	329(40)	172(48)	991(262)	294(47)	—	—	1,786(397)
W3552	8/6	2	47(36)	16(11)	93(84)	1(—)	1(—)	—	158(131)
W3052	9/22	2	—	6(1)	—	—	—	—	6(1)
W3050	8/5–9/23	2	1(1)	22(17)	16(3)	6(3)	—	—	45(24)
W3048	7/26–9/24	5	61(2)	13(—)	45(1)	72(44)	12(6)	—	203(53)
W2548	9/24	2	—	2(1)	1(—)	639(267)	106(18)	—	748(286)
Totals	5/24–9/24	129	7,933(4,706)	7,788(3,123)	6,926(1,807)	1,648(580)	165(48)	7(6)	24,467(10,270)
Totals, longline and seine combined		216	10,922(7,157)	8,768(3,888)	9,950(4,092)	1,786(659)	174(53)	56(40)	31,656(15,889)

[1] See Figure 1.

catches were much greater at stations on 57°30′N, as well as in the western half of the Gulf. Catches were comparable to catches made by Canadian longliners in 1962 (the previous cycle year), and larger in some cases.

(2) Associated with pink salmon in the southern Gulf early in May were immature sockeye, chum and chinook, maturing coho, and maturing as well as immature steelhead. These species also occurred farther northward as the season progressed.

(3) Maturing sockeye salmon were found mainly in a large area in the north central Gulf. Distribution was similar to that in 1962 and 1963. Their numbers decreased after about June 1, presumably as maturing fish emigrated coastward.

(4) Maturing chum salmon occurred in small numbers at most fishing stations, but not in concentrations, as did sockeye and pink. One set in area W5054 on July 15 yielded 175 chum salmon (mostly immature) on 20 skates of gear, which is considerably more than any previous catch of this species in the Gulf.

Operations in the Central Aleutian Area

Objectives were very satisfactorily carried out. The *Storm* repeatedly seined south of Adak at regular intervals from June 15 through August 15. Catch data are summarized in Table 2 by statistical area. The total of 65 index sets in area 8050 is nearly twice the number made in most previous years. The catches of immature sockeye were substantial, and indicate a good run to Bristol Bay in 1965. Most immature sockeye (93%) were 1-ocean age, as had been expected from the large downstream migration in Bristol Bay rivers in 1963. Scale readings also showed a high proportion (90%) of 2-winter *freshwater* age which was typical of the downstream migrants from the Kvichak River in 1963.

Most of the chum salmon taken in area 8050 (Table 2) were immature fish not due to return in 1964. Pink salmon were scarce in the Aleutian area, which is typical in an even-numbered year.

Operations in the Northeastern Gulf of Alaska

Seining for juvenile salmon in the northeastern Gulf was very successful, and objectives were well fulfilled. Table 2 lists the catches, most of which consisted of 0-ocean fish. The *Commander's* seine was modified in late July so that it would contain no web larger than 2½″ mesh stretched measure, 2″ mesh in the upper strips, and 1″ mesh in the bunt. From August 4 through September 25, the *Commander* fished a series of stations from Cape Flattery to Lituya Bay (58°N). Effort was greatest off Baranof Island. Sets were made from two miles offshore to 25 miles offshore, and opposed sets (NW *vs.* SE) parallel to shore were tried. Catches of 0-ocean salmon were made at nearly every location fished, in numbers ranging from just a few to over 1,200 per set. Catches from opposed sets indicated a strong northwest movement of 0-ocean salmon. Frequently, substantial numbers of mature salmon were taken in sets open northwest, but few, if any, 0-ocean fish. Sets open southeast, however, consistently took substantial numbers of 0-ocean salmon, sometimes accompanied by mature salmon. Since the net fished efficiently in either direction, the northward migration of 0-ocean fish was confirmed. Catches also indicated maximum abundance between five and 15 miles offshore. Few or none were taken at stations 25 miles offshore and within three miles of shore. Sockeye, chum, pink and coho salmon occurred in most catches, pink salmon predominating. The mean size of sockeye and chum salmon ranged from 13 to 18 cm, that of pink salmon from 12 to 18 cm. Coho salmon were larger, averaging between 20 and 24 cm.

The fine-meshed purse seine used by the *Commander* apparently retained all sizes of 0-ocean salmon in most sets. On two occasions when wind and tide collapsed the opening in the net, a number of the fish gilled, and presumably some escaped. When the net remained open in a normal set, however, it is doubtful that any fish escaped. The 1″ mesh size (knot-to-knot stretched measure) in the bunt precluded gilling in the bunt of any salmon in the size ranges encountered. Observations in the net using SCUBA gear indicated that if the net remains open, there seems to be no tendency for the fish to attempt to escape through the web. In fact, large schools of smelt and other fish smaller than salmon have also been retained and brailed from the bunt. Underwater observations during brailing showed, however, that larval fish 3–5 cm long found their way out of the bunt during brailing, but frequently many of these were captured by dip net before they could filter through the meshes.

TAG RETURNS

One sockeye tagged south of the central Aleutians on February 14 was recovered in Yakutat Bay on July 14. Another, released February 26 north of Adak, was recovered near 60°30′N, 175°E on July 29. These are the first returns from winter tagging in the Aleutian area. Additional tagging is needed before conclusions can be drawn.

Returns through January 31, 1965, from spring and summer operations will be presented for two major release areas: (1) from fish tagged west of 160°W (essentially area 8050) and, (2) from fish tagged in the Gulf of Alaska (east of 160°W).

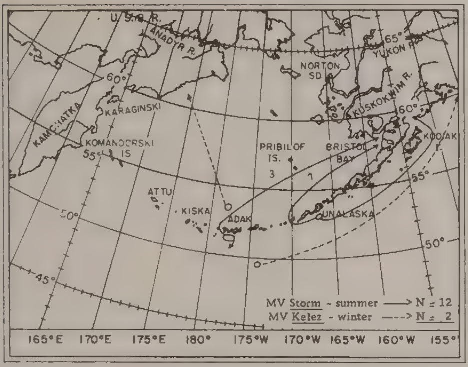
U.S.S.R.
ANADYR R.
NORTON SD.
YUKON R.
KUSKOKWIM R.
KAMCHATKA
KARAGINSKI
KOMANDORSKI IS.
PRIBILOF IS.
BRISTOL BAY
KODIAK
ATTU
KISKA
ADAK
UNALASKA
3
1
MV Storm - summer ——> N = 12
MV Kelez - winter ---> N = 2
165°E 170°E 175°E 180° 175°W 170°W 165°W 160°W 155°

FIGURE 2. Receovery distribution of mature sockeye salmon tagged west of 160°W in 1964.

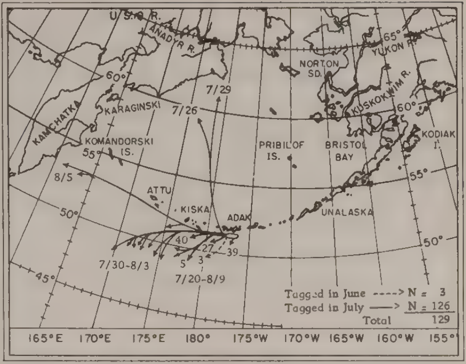
U.S.S.R.
ANADYR R.
NORTON SD.
YUKON R.
KUSKOKWIM R.
KAMCHATKA
KARAGINSKI
KOMANDORSKI IS.
PRIBILOF IS.
BRISTOL BAY
KODIAK I.
ATTU
KISKA
ADAK
UNALASKA
7/29
7/26
8/5
40
27
39
5
3
7/30-8/3
7/20-8/9
Tagged in June ---> N = 3
Tagged in July ——> N = 126
Total 129
165°E 170°E 175°E 180° 175°W 170°W 165°W 160°W 155°

FIGURE 3. Recovery distribution of .1 age immature sockeye salmon tagged and recovered in 1964.

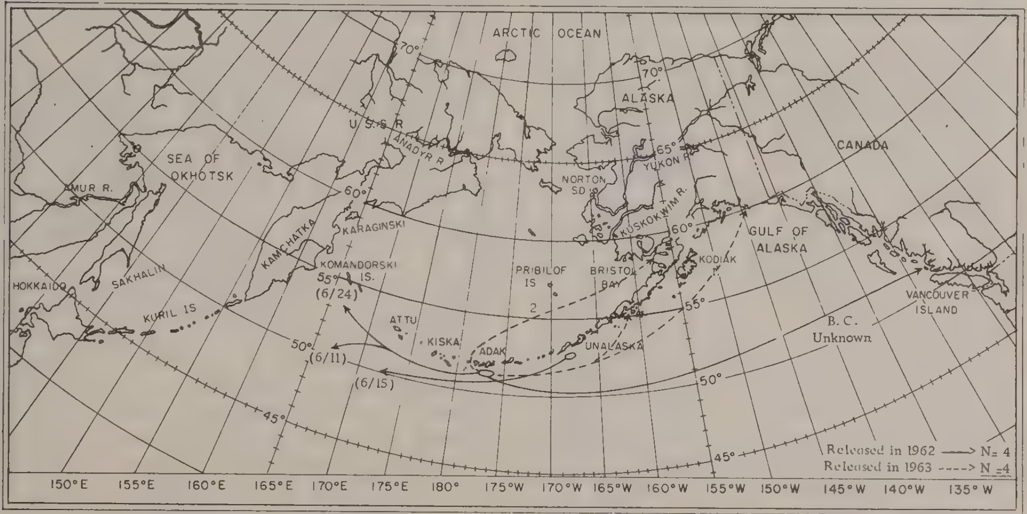
ARCTIC OCEAN
ALASKA
CANADA
U.S.S.R.
ANADYR R.
SEA OF OKHOTSK
AMUR R.
SAKHALIN
HOKKAIDO
KURIL IS.
KAMCHATKA
KARAGINSKI
KOMANDORSKI IS.
NORTON SD.
YUKON R.
KUSKOKWIM R.
GULF OF ALASKA
KODIAK
PRIBILOF IS
BRISTOL BAY
ATTU
KISKA
ADAK
UNALASKA
VANCOUVER ISLAND
B.C. Unknown
(6/24)
(6/11)
(6/15)
2
Released in 1962 ——> N = 4
Released in 1963 ----> N = 4
150°E 155°E 160°E 165°E 170°E 175°E 180° 175°W 170°W 165°W 160°W 155°W 150°W 145°W 140°W 135° W

FIGURE 5. Recovery distribution of sockeye salmon tagged in 1962 and 1963 and recovered in 1964.

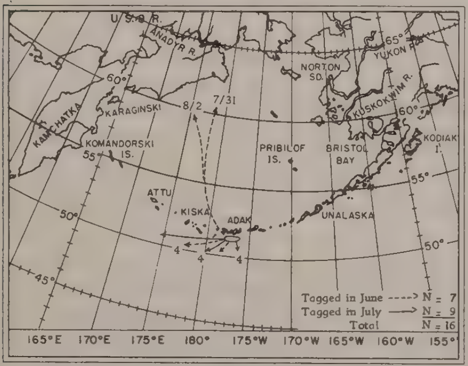
U.S.S.R.
ANADYR R.
NORTON SD.
YUKON R.
KUSKOKWIM R.
KAMCHATKA
KARAGINSKI
KOMANDORSKI IS.
PRIBILOF IS.
BRISTOL BAY
KODIAK I.
ATTU
KISKA
ADAK
UNALASKA
8/2
7/31
4
4
4
Tagged in June ----> N = 7
Tagged in July ——> N = 9
Total N = 16
165°E 170°E 175°E 180° 175°W 170°W 165°W 160°W 155°

FIGURE 4. Recovery distribution of .2 age immature sockeye salmon tagged and recovered in 1964.

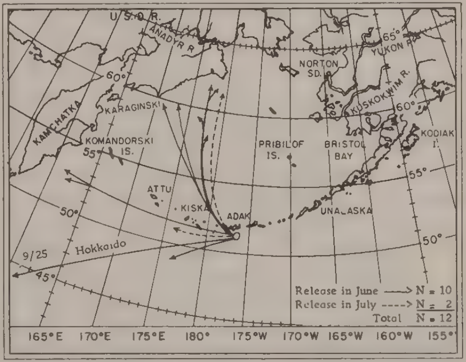
U.S.S.R.
ANADYR R.
NORTON SD.
YUKON R.
KUSKOKWIM R.
KAMCHATKA
KARAGINSKI
KOMANDORSKI IS.
PRIBILOF IS.
BRISTOL BAY
KODIAK I.
ATTU
KISKA
ADAK
UNALASKA
9/25
Hokkaido
Release in June ——> N = 10
Release in July ----> N = 2
Total N = 12
165°E 170°E 175°E 180° 175°W 170°W 165°W 160°W 155°

FIGURE 6. Recovery distribution of *mature* 3-year-old chum salmon tagged and recovered in 1964.

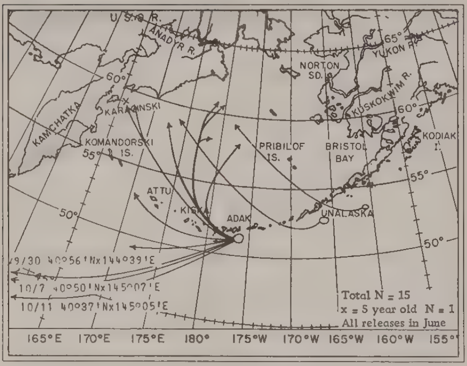
U.S.S.R.
ANADYR R.
65°
YUKON R.
NORTON SD.
60°
KUSKOKWIM R.
KAMCHATKA
KARAGINSKI
KOMANDORSKI IS.
55°
PRIBILOF IS.
BRISTOL BAY
KODIAK I.
ATTU
KISKA
ADAK
UNALASKA
50°
9/30 40°56'Nx144°39'E
10/7 40°50'Nx145°07'E
10/11 40°37'Nx145°05'E
Total N = 15
x = 5 year old N = 1
All releases in June
165°E 170°E 175°E 180° 175°W 170°W 165°W 160°W 155°

FIGURE 7. Recovery distribution of mature 4- and 5-year-old chum salmon tagged and recovered in 1964.

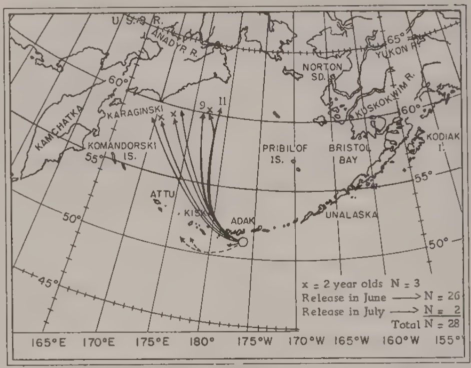
U.S.S.R.
ANADYR R.
65°
YUKON R.
NORTON SD.
60°
KUSKOKWIM R.
KAMCHATKA
KARAGINSKI
9
11
KOMANDORSKI IS.
55°
PRIBILOF IS.
BRISTOL BAY
KODIAK I.
ATTU
KISKA
ADAK
UNALASKA
50°
45°
x = 2 year olds N = 3
Release in June ——> N = 26
Release in July ——> N = 2
Total N = 28
165°E 170°E 175°E 180° 175°W 170°W 165°W 160°W 155°

FIGURE 8. Recovery distribution of immature 2- and 3-year-old chum salmon tagged and recovered in 1964.

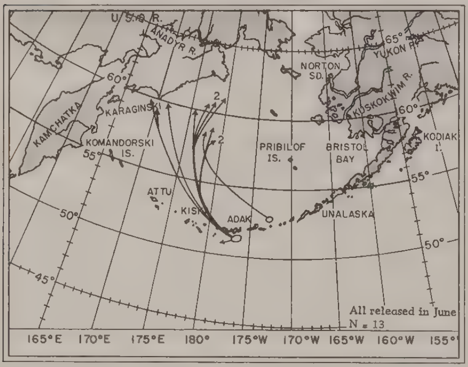
U.S.S.R.
ANADYR R.
65°
YUKON R.
NORTON SD.
60°
KUSKOKWIM R.
KAMCHATKA
KARAGINSKI
2
2
KOMANDORSKI IS.
55°
PRIBILOF IS.
BRISTOL BAY
KODIAK I.
ATTU
KISKA
ADAK
UNALASKA
50°
45°
All released in June
N = 13
165°E 170°E 175°E 180° 175°W 170°W 165°W 160°W 155°

FIGURE 9. Recovery distribution of immature 4-year-old chum salmon tagged and recovered in 1964.

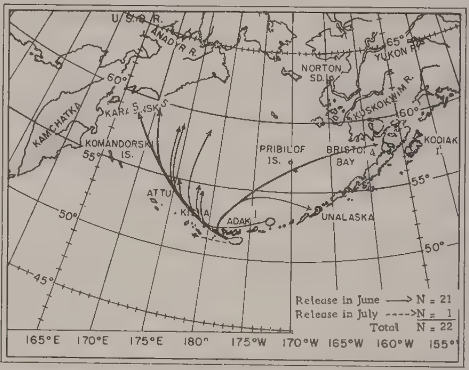
U.S.S.R.
ANADYR R.
65°
YUKON R.
NORTON SD.
60°
KUSKOKWIM R.
KAMCHATKA
KARAGINSKI
5
5
KOMANDORSKI IS.
55°
PRIBILOF IS.
BRISTOL BAY
KODIAK I.
ATTU
KISKA
ADAK
1
UNALASKA
50°
45°
Release in June ——> N = 21
Release in July ---->N = 1
Total N = 22
165°E 170°E 175°E 180° 175°W 170°W 165°W 160°W 155°

FIGURE 10. Recovery distribution of pink salmon tagged and recovered in 1964.

Releases West of 160° W

Figures 2 to 10 illustrate tag returns from releases west of 160°W for sockeye, chum and pink salmon.

Returns of mature sockeye salmon are shown in Figure 2. Of the 76 mature sockeye tagged near Adak in the summer, four (5.3%) were recovered. Since our main objective in the Aleutian area in 1964 was to sample and tag immature salmon, the first fishing at Adak was not until June 8, by which time the main body of matures had probably passed. The three returns to Bristol Bay and the one high seas return, therefore, probably represent the late part of the run. Tagging south of Unalaska was on June 6, probably close to the peak period of passage of mature sockeye salmon in this area. Of the 71 released, seven were returned from Bristol Bay and one from Cook Inlet (11.2%). Results are in agreement with those of earlier years.

The 1964 tag returns provided valuable new data on the migrations and rate of travel of immature sockeye annually passing westward through the central Aleutian area. In the past, only a few 1-ocean sockeye salmon had been recovered at sea late in the season, generally from areas near Attu Island. In 1964, however, the mothership fleet not only increased its late-season effort, but also made an unprecedented return to the central Aleutian area in late July and early August, with the result that a large number of tagged immature fish were taken close to the area of release as well as in more distant locations. The 129 recoveries (Figure 3) represent 3.5% of the 3,676 releases. Untagged fish of this size (30–40 cm) are not taken efficiently in the high seas gillnets, but tagged fish are held when the tag tangles in the threads.

Although the distribution of tag returns is largely a reflection of the distribution of the mothership fleet, it is evident from Figure 3 that immature sockeye passing through area 8050 disperse far and wide; westward to the Kamchatkan coast and northward to the vicinity of Cape Oliutorski-Cape Navarin. Hanamura (1964) has designated three areas of concentration of immature sockeye salmon: (1) off southeastern Kamchatka, of largely West Kamchatkan stocks, (2) off the Asian coast near Cape Oliutorski, of mainly East Kamchatkan stocks and, (3) in the central Aleutian area, of chiefly Bristol Bay stocks. The 1964 tagging results show a migration from the central Aleutians to the other two areas, suggesting an intermingling of Bristol Bay fish with the two Asian stocks close to the Asian coast. Such intermingling was indicated by the parasite studies of Margolis (1963). It is probably more pronounced in years when Bristol Bay sockeye are abundant, such as 1964. The relative strength of the migration to the various recovery areas is hardly indicated by Figure 3, since the distribution of the high seas fishing effort is not considered. Heavy interception by the fleet near the point of release would further influence the results. Daily catch and effort data, similar to those available for coastal fisheries, would be extremely valuable in interpreting high seas tag returns.

Recovery data in 1964 also provided new information on the rates of travel of 1-ocean sockeye. The four fish that were recovered farthest from the point of release (two westward and two northward, Figure 3) traveled 24, 25, 27, and 68 nautical miles per day, respectively. The last figure appears excessive and is probably due to an error in recovery data, but the average rate for the remaining three, 25.3 nautical miles per day, is not greatly less than that reported for mature sockeye (25–30 miles per day) tagged in the Adak area during their last 30–60 days at sea. The average rate of travel for all 128 sockeye of 1-ocean age was 17 miles per day; variations by days out and by distance traveled are detailed in Table 3.

More precise is the average speed (20–22 miles per day) for recoveries after 0–5 and 6–10 days at liberty, since presumably a direct relationship exists between unmeasured distance traveled (miles traveled other than in a straight line) and days at liberty. The progressively faster rate of travel according to miles traveled (Table 3, lower half) is undoubtedly due to an inverse relationship between miles wandered and straight-line distance between tagging and recovery points. The higher average rates for the more distant returns are probably biased too by the termination of the mothership fishing season on August 10. These rates probably represent only the faster fish, since the slower fish would not have had time to reach the more distant mothership fishing areas. Details of the daily positions and fishing effort of the mothership fleet are needed for adequate study of rate of travel.

The 1964 tag returns also provided data on the oceanic migrations of 2-ocean sockeye (illustrated in Figure 4). Fourteen of the 16 recoveries were from the area of tagging, or within 300 miles west of the point of release. Two migrated far to the north, as did two of the younger sockeye. Strangely, rate of travel averaged only 10 miles per day compared with 17 miles per day for the younger age group. Even the two older fish that traveled 500 miles or more averaged only 15 miles per day, compared with 25 miles per day for three reliable returns of younger fish that migrated far. A possible reason for the slower apparent rate for the older fish is their much longer average time at liberty (22.0 days compared with 12.5 days). This would allow for considerably more miles traveled in other than a straight line. The recovery rate for the older immatures was 5.1% (16 of 312 releases), compared to 3.5% for the younger fish.

The distribution of recoveries in 1964 of immature sockeye released in 1962 and 1963 is illustrated in Figure 5. The four released in 1962 were 1-ocean fish. Three were tagged with plastic darts, and one with a ½″ disc tag. The four 1963 releases were 2-ocean fish, and were tagged with ¾″ disc tags. The one recovered near the Komandorski Islands on June 24 was probably destined for an Asian stream. The coastal destination of the two recovered southwest of Attu Island on June 11 and 15 is less certain.

The returns of mature chum salmon are shown in Figures 6 and 7 according to age and month of release.

TABLE 3. Apparent rate of travel of immature 1-ocean sockeye salmon tagged in area 8050 and recovered at sea in 1964.

Rate of travel by days at liberty						
Days at liberty:	0–5	6–10	11–15	16–20	Over 20	All fish average 12.5 days
No. of returns	24	42	17	21	24	128
Average rate of travel (miles/day)	20.3	21.7	17.4	10.0	11.0	16.9
Rate of travel by miles traveled						
Miles traveled:	0–100	101–200	201–300	301–500	Over 500	All fish average 174.8 miles
No. of returns	32	61	19	12	4	128
Average rate of travel (miles/day)	11.6	15.5	29.0	28.0	35.6	16.9

Returns from the Soviet Union have not been received yet. The 3-year-old fish (Figure 6) yielded 12 high seas returns, mostly to the north and northwest of the point of release. The only coastal return was from Hokkaido. Most of the 4- and 5-year-olds were also recovered northwest of the release points (Figure 7), indicating a strong migration toward the northwest Bering Sea, a trend that had been evident in earlier years. Three were taken from the high seas off Hokkaido, and were probably destined for Japan or some nearby areas of the Soviet Union. Mature chum salmon were at liberty an average of 40 days before recovery, and traveled at an average apparent rate of 21 miles per day.

Immature chum salmon of all ages also migrated strongly to the northwest, as illustrated in Figures 8 and 9. Few were recovered in the area of tagging, or due west, in contrast to sockeye salmon. The difference in distribution by species is probably due to the fact that the majority (70%) of the chum salmon were tagged before July 1, whereas only 9% of the sockeye salmon were tagged by that date. The chum salmon therefore had greater opportunity to leave the area of tagging before arrival of the motherships in late July. The rate of travel for the 2-year-olds averaged 17 miles per day (37.6 days at liberty), and for the 3- and 4-year-olds, 20 miles per day (37.4 days at liberty).

Tags were returned for 22 of the 303 pink salmon released (7.3%), as shown in Figure 10. The general distribution of recoveries is typical for an even-numbered year; 17 were taken on a path toward Karaginski, four from Bristol Bay (Nushagak), and one from Unalaska Island. Returns may be expected from the Soviet coastal fishery.

Releases in the Gulf of Alaska

Tag returns from Gulf of Alaska tagging are shown in tabular form for simplicity (Tables 4 to 6). Recoveries from Aleutian experiments are included for

TABLE 4. Summary of sockeye salmon returns from 1964 tagging.

	Tagging area[1]																							
Recovery area	8050	W7052	W6054	W5556	W5554	W5552	W5550	W5548	W5056	W5054	W5052	W5050	W5048	W5046	W4556	W4554	W4552	W4550	W4548	W4056	W4054	W4052	W4050	W3554	Total
High seas	146	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	1	—	—	—	—	—	149
Togiak	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1
Nushagak	—	2	1	—	2	2	—	—	—	1	4	—	—	—	—	4	—	—	—	—	—	—	—	—	16
Naknek-Kvichak	3	4	1	—	1	2	—	—	—	2	3	—	—	—	—	1	1	—	—	—	—	—	—	—	18
Egegik	—	1	—	—	—	1	1	—	—	—	1	—	—	—	—	2	—	—	—	—	—	—	—	—	6
Ugashik	—	—	—	1	—	—	—	—	—	2	1	—	1	—	—	—	—	—	—	—	—	—	—	—	5
Alaska Pen.																									
North side	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—		—	—	—	—	—
South side	—	—	—	2	1	—	—	—	2	8	1	—	—	—	—	1	1	—	—	—	—	—	—	—	16
Kodiak I.	—	—	—	—	—	—	—	—	1	1	—	—	1	—	1	—	—	—	—	—	—	—	—	—	4
Cook Inlet	—	1	—	1	—	—	—	—	—	1	—	—	—	—	—	5	2	—	—	—	—	—	—	—	10
Copper &																									
Bering R.	—	—	—	—	1	1	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	3
Yakutat	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	—	—	—	—	—	—	—	1	3
Southeast Alaska																									
Icy Straits	—	—	—	—		—	—	—	—	—	—	1	—	—	1	2	—	—	—	—	1	—	—	1	6
Chatham	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	1
Petersburg	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1
Pr. of Wales	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	3	1	—	—	—	3	—	—	—	8
Ketchikan	—	—	—	—	—	—	—	1	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2
Nass River	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	1	—	—	—	—	—	—	—	—	2
Skeena River	—	—	—	—	1	—	—	—	1	7	—	—	—	—	3	5	—	—	—	—	7	—	—	1	25
B. C. (N of 52°N)	—	—	—	—	—	—	—	—	1	3	—	—	—	—	1	7	—	—	—	1	1	—	—	—	14
B. C. (S of 52°N)	—	—	—	—	—	1	1	—	1	7	2	1	2	—	—	9	6	4	2	1	—	1	2	—	40
Fraser River	—	—	—	—	—	1	1	—	—	—	1	—	1	1	1	—	1	1	1	—	—	1	1	—	11
Puget Sound	—	—	—	—	—	—	—	—	—	—	—	2	1	—	—	1	—	—	1	—	—	1	—	—	6
Total	149	8	2	4	6	8	3	1	6	38	13	4	6	1	8	43	12	7	5	2	12	3	3	3	347

[1] See Figure 1.

TABLE 5. Summary of chum salmon returns from 1964 tagging.

Recovery area	Tagging area[1)																		
	8050	W7552	W7052	W6552	W5556	W5554	W5552	W5548	W5056	W5054	W4556	W4554	W4552	W4548	W4058	W4056	W4054	W3554	Total
High seas	66	1	1	1	—	—	—	1	—	—	—	—	—	—	—	—	—	—	70
Yukon River	—	—	—	—	—	2	1	—	1	—	—	1	—	—	—	—	—	—	5
Kuskokwim R.	—	—	—	—	1	—	1	—	—	—	—	—	1	—	—	—	—	—	3
Togiak	—	—	—	—	—	1	—	—	1	—	—	—	—	—	—	—	—	—	2
Nushagak	—	—	—	—	1	1	—	—	1	1	—	—	—	—	—	—	—	—	4
Alaska Pen. South side	—	—	—	—	1	—	—	—	—	1	2	—	—	—	—	—	—	—	4
Kodiak	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	1	—	2
Cook Inlet	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	1
Southeast Alaska																			
Icy Straits	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	1
Pr. of Wales	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	1
B. C. (N of 52°N)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	1
Fraser River	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	1
Puget Sound	—	—	—	—	—	—	—	—	—	—	1	—	—	1	1	—	—	—	3
Total	66	1	1	1	4	4	2	1	4	2	4	1	1	1	2	—	2	1	98

1) See Figure 1.

TABLE 6. Summary of pink salmon returns from 1964 tagging.

Recovery area	Tagging area[1)																	
	8050	W7552	W5556	W5056	W5054	W5048	W5046	W4556	W4554	W4550	W4546	W4058	W4056	W4054	W3554	W3552	W3550	Total
Total tagged	*297*	*2*	*119*	*119*	*150*	*39*	*38*	*172*	*420*	*18*	*83*	*31*	*434*	*620*	*269*	*82*	*10*	*2903*
High seas	16	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	17
Nushagak	4	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	4
Aleutian Is.	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1
Alaska Pen. South side	—	—	1	1	2	—	—	—	—	—	—	—	—	—	—	—	—	4
Kodiak I.																		
Gulf side	—	—	3	1	3	—	—	2	1	—	1	—	—	—	—	—	—	11
Shelikof side	—	—	1	1	3	—	—	1	2	—	2	—	—	—	—	—	—	10
Cook Inlet	—	—	1	2	1	—	1	6	6	1	2	—	—	3	—	—	—	23
Pr. William Sd.	—	—	5	—	—	1	—	—	2	—	—	—	—	3	—	—	—	11
Yakutat	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Southeast Alaska																		
Unknown	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	1
Icy Straits	—	—	—	—	—	—	—	—	1	—	—	2	9	5	—	—	1	18
Chatham	—	—	—	—	—	—	—	—	—	—	—	—	3	1	5	1	—	10
Petersburg	—	—	—	—	—	—	—	—	—	—	—	1	6	3	8	—	—	18
Pr. of Wales	—	—	—	—	—	—	—	3	1	—	—	—	10	9	14	3	—	40
Ketchikan	—	—	—	1	—	—	—	1	—	—	—	—	3	1	5	—	—	11
Nass River	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	1
Skeena River	—	—	—	—	—	—	—	—	1	—	—	—	2	1	3	5	—	12
B. C. (N of 52°N)	—	—	—	—	—	—	—	1	2	—	—	—	—	1	11	5	—	20
B. C. (S of 52°N)	—	—	—	—	—	—	—	—	—	—	—	—	1	—	2	—	—	3
Puget Sound	—	—	—	—	—	—	—	—	—	—	—	—	1	—	1	—	—	2
Total	21	1	11	6	9	1	1	14	16	1	5	3	36	27	50	14	1	217

1) See Figure 1. (Only those tagging areas which yielded returns are shown.)

completeness.

Sockeye salmon recoveries were widespread (Table 4) as in previous years. Of particular interest are three immature sockeye released in the central Gulf (areas W4548 and W4550) that were recovered at sea near Adak by the mothership fleet. One was tagged on May 8 and two on May 22. Recovery was on July 26, July 28 and August 3. All were 2-ocean age and between 39.5 and 44.5 cm at release. These three returns show that some of the immature sockeye passing westward in the central Aleutians come from as far away as the central Gulf (1,200 miles). The rate of travel ranged from 16 to 22 nautical miles per day.

There were only 29 chum salmon returns from Gulf experiments (Table 5). As in previous years, there was a general mixing of fish from many sources throughout much of the Gulf.

There were 195 pink salmon returns from Gulf releases (Table 6), or 7.0% of all mature pinks released in the Gulf (2,771), which compares favorably with the 7.3% return from Aleutian experiments. As in previous years, the rate of return was much lower for the early-season releases far from the coast than for late-season releases closer inshore.

Gulf releases of mature coho salmon yielded nine returns, eight of which were tagged close to the coasts of Washington State and Southeastern Alaska, and were recovered along the same general coastal strip. A longer migration is shown by one that was tagged at 47°N, 146°W (May 25) and recovered in the Kuskokwim River (August 20). Releases of immature coho salmon yielded eight returns. These fish were 25–30 cm long and were tagged north of Cape Flattery on September 24. Recovery was between September 28 and October 21 from the Strait of Juan de Fuca and in Puget Sound.

There were no chinook salmon returns.

Three tagged steelhead were returned, all captured in rivers with rod and reel. Two tagged at 49°N, 146°W on May 26 were recovered, respectively, in the Willapa River, Washington, on December 10, 1964, and the Alsea River, Oregon, in January 1965. The third, released at 47°N, 146°W on May 25, was recovered in the Carmel River, California (36°30′N, 123°00′W) on January 27, 1965.

Tag Recovery Effort

A new reward scheme was tried in 1964 in an effort to obtain lengths and scale samples from more of the recovered fish, and to impress fishermen with the value of tag returns from fish tagged as immatures one or two years earlier. The standard reward of $1.00 was offered for 1964 recoveries of fish tagged in 1964, $10.00 for fish tagged in 1963 and $25.00 for fish tagged in 1962 or earlier.

Advertising posters and tag return envelopes were distributed as in previous years. In addition, information leaflets addressed to fishermen were printed and distributed widely through canneries, fishery agencies, unions, and directly to individuals by mail. Representatives of the tagging project visited Bristol Bay canneries during the peak of the season, and the system of paying an individual at each cannery for each tag processed was continued.

Personnel of the Alaska Department of Fish and Game, the U.S. Bureau of Commercial Fisheries and the Washington State Department of Fisheries rendered valuable help in forwarding tags and information. Canada also promptly forwarded information and tags from fish recaptured by Canadian fishermen. Japan forwarded tags and related data at the annual meeting in Tokyo in November 1964. Tags recovered by Soviet fishermen have not been received at the time of writing.

Tags and Methods

Standard disc tags, $\frac{3}{4}''$ in diameter, half red and half white, were used on all mature fish and on all immatures to a minimum length of 30 cm (those which had spent one year or more at sea). Discs were affixed with the crimping plier described in the 1963 report. Dart tags identical to those used in 1963 were attached to the 0-ocean fish. These were made of $\frac{1}{16}''$ plastic tubing $2\frac{1}{2}''$ long, attached to a single-barbed nylon point, and inserted with a hollow needle alongside the dorsal fin, with the protruding tube trailing posteriorly from the dorsal surface. These fish were anesthetized with M.S. 222. Few scales were lost and fish appeared in good condition at release. Some returns may thus be expected in future years.

Snap-Gangen Longlines

A test was made during May of a snap-gangen type of surface longline, in which 10,000 feet of mainline (braided nylon No. 36) was set from a reel, and baited gangens and floats were attached by stainless steel wire clips as the line was fed out. During retrieval the line was cranked directly back on the reel, and the gangens and floats were unsnapped and placed in racks ready for the next set. The principal advantage expected was elimination of the time required to overhaul and recoil the standard surface longline (approximately two hours for six men fishing 20 skates).

The system worked satisfactorily in most respects, but there proved to be little or no saving in overall time. Setting, as had been expected, took longer (40 minutes per 1,000 hooks compared to 20 minutes for standard gear). Retrieving, however, required three hours, compared to 1½ hours for standard gear, and more personnel, because of the necessity of rapidly placing gangens back in their racks. This interfered with fish handling and tagging. Tangling of some gangens in the stainless steel clips contributed to the delay. Finally, there was a 10% unexplained loss of gangens because of either improper seating of the clips during setting, or because of fish fouling the gangen on the clip in such a manner that the clip could become dislodged. Clips on which fish were caught appeared satisfactory, and showed no tendency to slide or to become dislodged.

The test showed that with practice the method is workable, but since it offered no real advantages over the standard gear, it was discontinued after the single trial. From the standpoint of fishing effectiveness, there is no reason to expect the snap-gangen line to be any different from the standard line. The catch in this test set on May 14 was 36 salmon, based on the equivalent of 13 skates of gear retrieved, which is reasonable with respect to catches in adjacent areas at this period.

Sonic Tag Tests

Preliminary tests were conducted on the feasibility of following salmon at sea by means of sonic tags. Sonic " pinger " tags developed by the Bureau of Commercial Fisheries Fish-Passage Research Program in Seattle were used, together with portable " sniffers " and probes kindly lent for our purposes by the above group. Tests in harbors near Adak showed that salmon can easily be followed by means of sonic tags and probes, and that a single skiff and detecting unit is sufficient to maintain contact for several hours. Actual studies of fish movements at sea were not conducted because of weather conditions and fog, but the tests indicate no mechanical difficulty in such application.

Longlining for Juvenile Salmon

The testing of longlines with small hooks and baits for catching 0-ocean salmon was rendered unnecessary by the success of purse seining for this purpose. Moreover, the prevalence of mature salmon as well as sharks in the same waters would probably nullify the effectiveness of such gear for the small salmon. In this regard, it is interesting that the stomachs of mature salmon contained no 0-ocean salmon even in areas where both were prevalent. Smelt and other small fish were common in the salmon diet. Some of the young salmon, however, had injuries apparently caused by predator fish.

Tests of Dart Tags

The dart tags (described earlier) appear to be satisfactory for salmon of 0-ocean age, but an improved tool for applying the tag would be desirable. This is the first year that substantial numbers of this age group have been tagged at sea, so that returns in 1965 should indicate the success or failure of the tag. Tests at a local trout farm show a high percentage of shedding, but the physiological processes for tag retention and anatomy of salmon in salt water may be quite different. Actual field tests should be conducted.

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SALMON DISTRIBUTION AND ABUNDANCE STUDIES

by Robert R. French

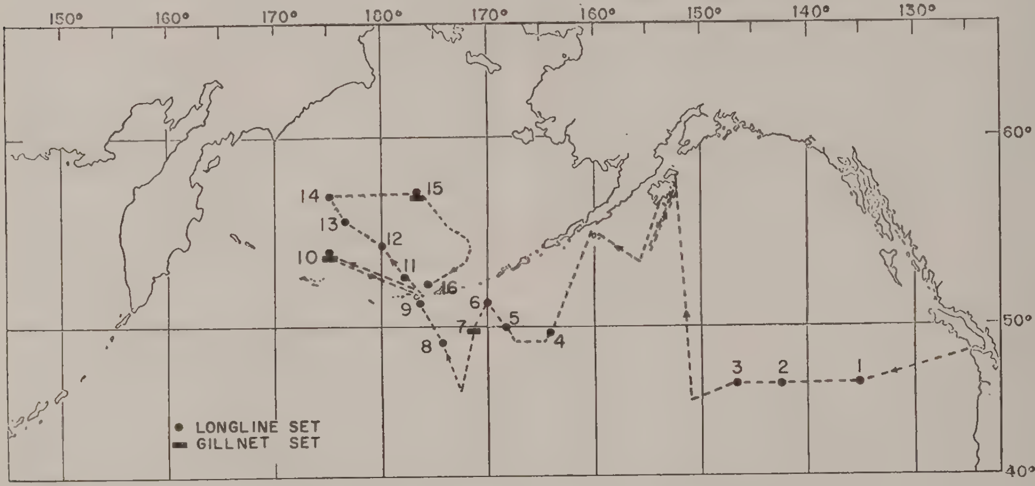
Research on high seas salmon distribution and abundance was continued in 1964. Winter and late summer fishing cruises were conducted using the research vessel of the Bureau of Commercial Fisheries, the *George B. Kelez*.

The winter cruise was planned in cooperation with Canada. The objectives of both national sections were (1) to describe the distribution and abundance of salmon populations and (2) to determine origins and movements of salmon by means of tagging experiments. The Canadian vessel occupied stations in the Gulf of Alaska from the North American coast to longitude 155°W. Results of the Canadian cruise have been reported by Manzer and Dodimead (1964).

The United States vessel fished stations in the North Pacific Ocean between longitudes 160°W and 180°. Severe storms during much of the cruise and an engine failure prevented the *Kelez* from completing the station pattern assigned to the United States. The winter cruise track and station pattern are illustrated in Figure 11. Results of the tagging experiment are reported in the previous section, " Tagging Studies ", by the Fisheries Research Institute, University of Washington, which did the study under contract to the Bureau of Commercial Fisheries.

The summer fishing cruise was planned to increase our knowledge of the distribution and relative abundance of immature sockeye and chum salmon in the western North Pacific Ocean. Of special interest was the determination of their westward limits of migration. Other objectives were (1) to compare the effectiveness of the gillnet and longline gear in taking the various age groups of salmon and (2) to assess the loss of fish from gillnets on the high seas. Stations occupied during the summer cruise are illustrated in Figure 12.

The following report will discuss the results of these winter and summer cruises. Results of longline fishing in the winter cruise of 1964 are compared to those results of winter fishing in 1962 and 1963. In addition, progress is reported on related high seas salmon studies of (1) visceral adhesions in high seas salmon, (2) separation of immature salmon "subpopulations" by means of age ratios and (3) salmon distribution in the Gulf of Alaska.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170°
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3
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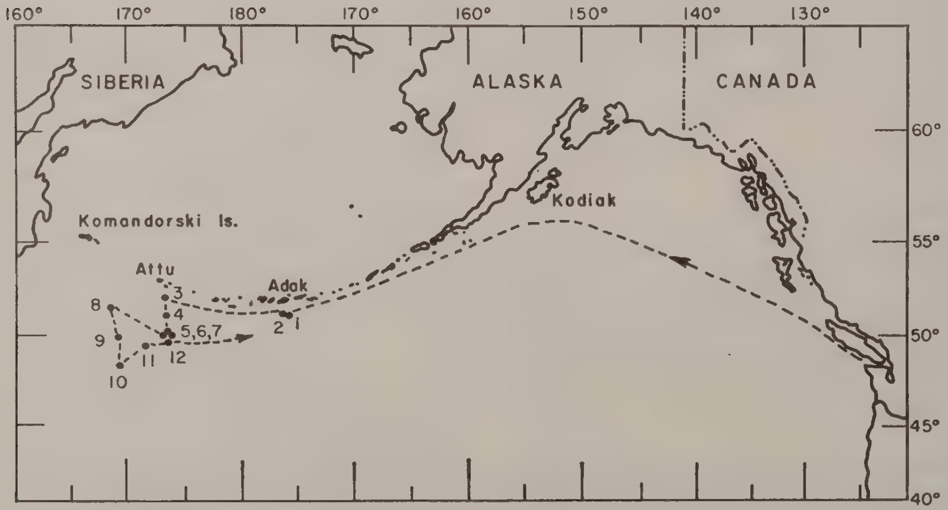
7
8
9
10
11
12
13
14
15
16
● LONGLINE SET
▬ GILLNET SET

FIGURE 11. Cruise track and fishing stations of the *George B. Kelez*, January 17—March 18, 1964.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SIBERIA
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CANADA
Kodiak
Komandorski Is.
Attu
Adak
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5,6,7
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12

FIGURE 12. Cruise track and fishing stations of the *George B. Kelez*, August 20—October 22, 1964.

Fishing Gear and Methods

Most of the salmon taken during the winter cruise of the *Kelez* were caught by Japanese longline gear. A standard longline set consisted of 30 skates of gear. Each skate (hachi) was about 355 feet in length and contained 49 hooks spaced about seven feet apart. Gangens measured 33 inches in length. Two hook sizes were fished: Japanese designation T-8 and, on on occasion, T-6 (approximate United States sizes 1/0 and 4). The first 20 skates provided salmon for tagging and the remaining 10 skates provided samples for certain biological information. The number of skates set at each station was reduced in marginal fishing weather.

Normally, the longlines were set just before dawn and hauled after a one-half hour soak. Gear was set at the rate of about one skate per minute. Hauling took approximately five minutes per skate or about 2½ hours for 30 skates. After an initial gear familiarization period, the crew members recoiled baskets of gear and rebaited hooks at the rate of approximately three-quarters of a man-hour per skate.

Because of continually stormy weather during the winter cruise, comparisons of longlines and gillnets were made only on two occasions. These gillnet strings consisted of 24 multifilament nets, 12 each of 4½″ and three each of 5¼″, 3¼″, 2½″ and 2″ mesh nets.

During the late summer cruise, gillnets were the principal fishing gear with longlines being fished only on two occasions for comparative purposes. The standard gillnet string used for distribution studies consisted of 24 nets, 12 each of 4½″, and four each of 5¼″, 3¼″ and 2½″ mesh nets. The longline gear was identical with that fished during the winter cruise.

Also during the summer cruise, a special gillnet string of four units of gear (a unit consisted of two 50-fathom shackles each of 4½″ and 3¼″ mesh nets) was fished to study loss of fish from gillnets. These gillnet units were set, hauled and reset at intervals throughout the night. Catch comparisons were made (1) among nets fished for different time periods during the night and (2) among nets fished continuously for 6, 9 and 12 hours and nets in which catches were summed for shorter time periods.

Winter Cruise Results

Salmon and steelhead catches and associated data are given in Table 7 by set number. Only salmonids were caught in the 1964 winter cruise.

Distribution and Relative Abundance

Sockeye salmon were taken at every station fished in the Aleutian area (Figure 13). The relatively few

Table 7. Salmon and steelhead catches, *George B. Kelez* winter cruise, 1964.

Set no.	Date	Position		Surface temp. (°C)	Gear[1]		Species				Total
		Lat.	Long.		Kind	Number	Sockeye	Chum	Pink	Steelhead	
1[2]	1/20	46°31′N	133°37′W	8.9	LL	10	—	—	—	17	17
2	1/22	46°30′N	142°09′W	7.4	LL	20	—	—	15	1	16
3	1/23	46°30′N	148°32′W	6.9	LL	20	—	—	9	—	9
4	2/9	49°50′N	163°55′W	4.2	LL	29	97	—	—	—	97
5[2]	2/10	49°55′N	168°46′W	3.9	LL	10	5	—	—	—	5
6	2/11	51°42′N	170°03′W	3.2	LL	20	25	—	—	—	25
7	2/12	49°50′N	170°50′W	3.8	GN	24	20	1	—	—	21
8	2/14	49°03′N	174°20′W	3.3	LL	30	52	—	—	—	52
9	2/15	51°20′N	176°03′W	3.8	LL	30	6	—	—	—	6
10	2/22	54°15′N	175°58′E	2.0	LL	10	4	—	—	—	4
	2/22	54°15′N	175°58′E	2.0	GN	24	7	—	—	—	7
11	2/26	52°53′N	178°05′W	3.2	LL	20	5	—	—	—	5
12	2/29	54°30′N	180°	1.5	LL	20	14	—	—	—	14
13	3/1	56°00′N	176°26′E	1.0	LL	20	5	—	—	—	5
14	3/2	57°00′N	175°00′E	0.0	LL	20	9	—	—	—	9
15	3/4	57°00′N	177°00′W	1.8	LL	20	3	—	—	—	3
	3/4	57°00′N	177°00′W	1.8	GN	24	1	—	—	—	1
16	3/8	52°25′N	175°27′W	2.6	LL	30	10	—	—	—	10
						Totals	263	1	24	18	306

[1] LL = skates of longline.
GN = shackles of gillnet.

[2] Day set.

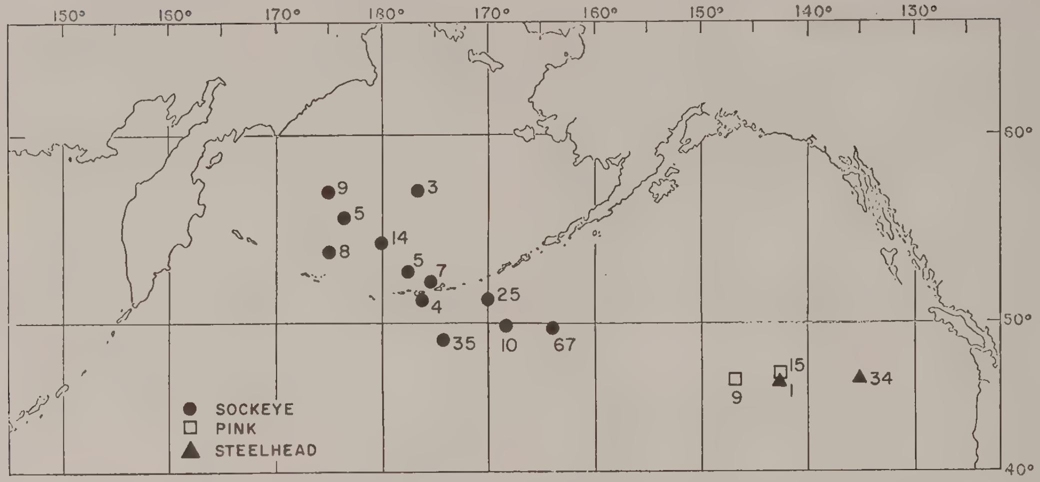

FIGURE 13. Distribution of salmon and steelhead catches by longline gear, *George B. Kelez* winter cruise, 1964. (Numerical values represent catches weighted to 1,000 hooks.)

stations fished, however, preclude making more than general statements about the winter distribution patterns of this species. Sockeye salmon appeared to be more abundant in the North Pacific Ocean than in the Bering Sea. In particular, the catches near latitudes 49°N and 50°N showed a westward extension of the abundance centers noted previously in the central and western areas of the Gulf of Alaska (French and Mason, 1964; Fisheries Research Board of Canada, 1964b). These reports have shown sockeye salmon to be widely distributed across the North Pacific Ocean during winter months, extending from the eastern part of the Gulf of Alaska to at least longitude 180° in the central North Pacific Ocean.

In the Bering Sea, longlines caught sockeye salmon in all areas sampled. These catches cannot be compared with abundance indices obtained during previous year's gillnet catches. Catches in 1964 confirmed, however, that the winter habitat of sockeye extends northward to at least latitude 57°N between longitudes 175°W and 175°E.

We have found sockeye salmon in the central Aleutians area during at least eight months of the year (May-September, January-March). In all probability, some age groups of this species are to be found there in every month of the year.

The 1964 winter fishing produced only one chum salmon. This was a small specimen (239 mm) taken in the gillnet set at 49°50′N, 170°50′W. The apparent low abundance of chum salmon may be explained by lack of sampling in chum salmon waters. During previous winter cruises, chum salmon were taken mainly between latitudes 47°N and 49°N, and also east and west of the area fished in 1964.

The only pink salmon captured were those taken at the two stations along latitude 46°30′N, between 750 and 900 miles offshore. They are known to be abundant in this area in early spring (Fisheries Research Board of Canada, 1964a, 1964b).

Steelhead occurred only at two stations about 360 and 725 miles off the coast of Washington State. The catch of 17 fish at Station 1 (34 fish when weighted to 1,000 hooks) was comparable to Canadian catches in this general area in April 1963 (Fisheries Research Board of Canada, 1964b).

Length and Age Composition

Length frequencies of winter sockeye salmon revealed a fairly distinct size separation of the fish by number of winters at sea (Figure 14). Average lengths (in mm) of sockeye salmon taken in the Aleutian area in the 3-year period 1962–64 are compared below. The 1- and 2-winter-at-sea sockeye taken in 1964 were smaller than those captured in 1962 and 1963. The 3-winter fish were comparable in size for all years.

Year	*1-winter-at-sea*	*2-winter-at-sea*	*3-winter-at-sea*
1962	274.7	483.5	535.6
1963	286.3	464.7	549.8
1964	250.7	463.8	542.9

Difference in size was also related to the area in which the salmon were caught. Bering Sea sockeye were, on the average, longer than those taken in the

North Pacific (see Table 8).

Distribution of the different age groups of sockeye salmon (Figure 15) showed that the younger age groups decreased as sampling moved westward and to the north. Only two specimens of the 1-winter age group were taken in the Bering Sea, at Station 16 just north of the Aleutian Islands.

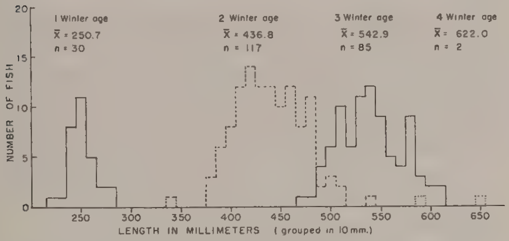

FIGURE 14. Length frequencies of sockeye salmon by number of winters at sea, *George B. Kelez* winter cruise, 1964.

Pink salmon, all in their second year of life, were 225 mm to 390 mm long, with an average length of 300.4 mm for 24 fish. Fish taken in gillnets in 1962 and 1963, in areas farther to the west, were 288 mm to 379 mm long, a narrower size range than that obtained for the 1964 longline-caught fish.

The 18 steelhead taken on longlines were mostly small fish ; 16 were in their first winter at sea and two were in their second. The younger fish averaged about 427 mm in length and the older fish 623 mm.

Maturity

Normally, the onset of maturity cannot be detected in winter-caught salmon by visual observation of gonads. To obtain data on maturity of sockeye salmon, we sent blood samples taken from female sockeye salmon to the laboratory for serological examination (see Ridgway, Klontz and Matsumoto (1962) for method). The examination indicated onset of maturation in about 89% (32 of 36) of the older female sockeye salmon (2-, 3- and 4-winter-at-sea) examined. Approximately equal numbers of females in the age groups 4_2, 5_3, 5_2 and 6_3 showed onset of maturation. One specimen was age 7_3. Of the four sockeye not showing onset of maturation, two were age 4_2 and two were age 5_3. This does not necessarily mean that these female sockeye salmon would not have spawned the following autumn ; the serological tests indicated only that there was no evidence of maturation in the specimens on the date of examination.

TABLE 8. Average fork lengths in millimeters of winter sockeye by age groups[1] and area.

Area and sets	*1-winter-at-sea* 4_3	3_2	*2-winter-at-sea* 4_2	5_3	*3-winter-at-sea* 5_2	6_3
North Pacific	250.4	250.4	427.9	438.5	533.5	534.6
Sets 4–9	(250.4)		(432.5)		(534.0)	
Bering Sea	256.0		—	488.8	563.1	560.7
Sets 10–16	(256.0)		(488.8)		(562.1)	

[1] Age groups combined in parentheses.

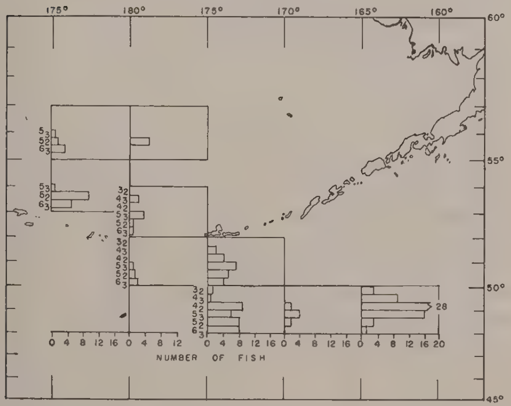

FIGURE 15. Distribution of sockeye salmon catches by age groups, *George B. Kelez* winter cruise, 1964. (Catches weighted to 1,000 hooks and data combined for 2° × 5° areas.)

The pink salmon in the winter catches of 1964 would have spawned in that year since they were in their second year of life. We have no data for judging whether or not the steelhead would have matured. Steelhead usually return as matures after two winters at sea. Since most of the steelhead were caught far offshore during their first winter at sea, it is doubtful they would have returned to spawning streams that same winter as jacks. Most likely they would have returned as matures the following winter.

Environmental Relationships

Data obtained during the winter cruises of 1962 and 1963 illustrated to some degree a relationship between the occurrence of salmon species and surface water temperatures. Sockeye salmon were caught in surface water temperatures as low as 2.4°C, the minimum encountered in the Bering Sea. Pink and coho salmon were found mainly in waters with surface temperatures ranging from 5.5°C to 8.9°C, although pink salmon occurred in two sets at surface water temperatures of 3.5°C and 3.7°C. Chum salmon were caught in surface water temperatures ranging from 3.4°C to 8.0°C. During 1964, sockeye salmon again appeared in the coldest surface waters fished, 0°C at latitude 57°N in the Bering Sea. Pink salmon and steelhead were taken in the warmest surface waters. (See Table 7.)

Sampling north and south along various longitudes during the 1964 winter cruise was insufficient to relate salmon distribution with sub-surface temperature and salinity structures described for previous winter cruises (Favorite, 1964; Favorite and Morse, 1964).

Gear Comparisons

The winter cruise included fishing with both longlines and gillnets at similar times and places in order to compare selective features of the two forms of gear. Because of continual rough weather only two comparative sets were accomplished. These results were inconclusive. In set No. 10, gillnets caught seven sockeye salmon and longlines took four; in set No. 15, gillnets caught one sockeye and longlines caught three.

At Station 7, in the North Pacific Ocean, gillnets were set at 11:00 p.m., with longline gear prepared for a dawn set. Unfortunately, strong winds at dawn prevented setting the longline gear. The gillnet catch of 20 sockeye salmon was, however, interesting to compare with the longline catches at other stations (4, 6 and 8) in the general area. Whereas small, 1-winter-at-sea fish comprised only 13% of the longline catch, they comprised 50% of the gillnet catch.

Normally, large hooks were used on the longline gear. For experimental purposes, we tested a small hook during two different sets (Table 9). Apparently, the smaller hooks were selective for small, 1-winter-at-sea fish. Thus, if more of the fishing effort had

Table 9. Comparison of sockeye salmon catches with small and large hooks, winter cruise, 1964.

	Small hooks					Large hooks				
Set no.	No. of skates	Total catch (no.)	2-, 3-, 4-winter-at-sea	1-winter-at-sea	Percent 1-winter-at-sea	No. of skates	Total catch (no.)	2-, 3-, 4-winter-at-sea	1-winter-at-sea	Percent 1-winter-at-sea
4	5	29	15	14	48.3	24	68	64	4	5.9
8	5	10	8	2	20.0	25	42	41	1	2.4

Table 10. Salmon catches, *George B. Kelez* summer cruise, 1964.

Set no.	Date	Position		Surface temp. (°C)	Gear[1]		Catch					
		Lat.	Long.		Kind	No.	Sockeye	Chum	Pink	Chinook	Coho	Total
1	9/2	51°33′N	176°18′W	7.5	GN	22	74	3	—	1	—	78
2[2]	9/5	51°33′N	176°18′W	8.1	GN	16	73	33	—	—	—	106
3	9/26	52°10′N	173°00′E	6.9	GN	24	16	6	—	—	—	22
4	9/27	51°10′N	173°00′E	7.9	GN	24	47	20	—	—	—	67
5	9/29	50°10′N	173°00′E	7.2	GN	24	147	219	—	1	—	367
	9/29	50°12′N	173°04′E	7.2	LL	20	33	88	—	—	—	121
6[2]	9/30	50°10′N	173°00′E	7.0	GN	28	127	128	—	1	1	257
7[2]	10/2	50°10′N	173°00′E	6.6	GN	28	185	54	—	—	—	239
8	10/7	51°55′N	168°26′E	7.5	LL	20	20	6	—	—	—	26
9	10/8	50°00′N	169°00′E	6.9	GN	24	23	159	1	2	1	186
	10/8	49°56′N	168°52′E	6.9	LL	20	14	14	—	—	—	28
10	10/9	48°30′N	169°00′E	7.6	GN	24	13	83	—	—	—	96
11	10/10	49°50′N	171°30′E	6.3	LL	28	6	10	—	—	1	17
12[2]	10/11	50°10′N	173°00′E	6.5	GN	28	59	42	—	1	—	102
						Totals	837	865	1	6	3	1,712

[1] GN=shackles of gillnet.
LL =skates of longline.

[2] A special net string was fished in which individual gear units were set and hauled after varying periods of fishing.

consisted of small hooks, we might have taken a greater number of small fish in the areas covered during the 1964 winter cruise.

Summer Cruise Results

Fishing results of the summer cruise with associated data are listed in Table 10 by set number.

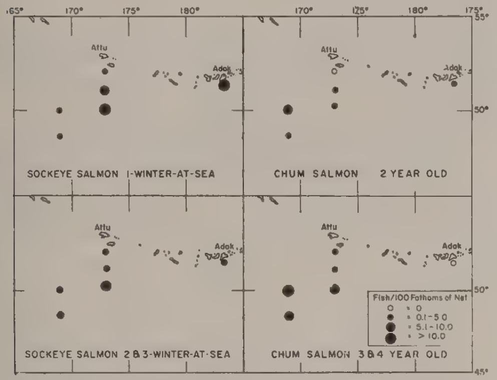

Figure 16. Relative abundance of sockeye and chum salmon, September-October, 1964.

Distribution and Relative Abundance

Although the ocean area covered in September and October was not extensive, catches of sockeye and chum salmon provided new information on their distribution and relative abundance in the high seas. Previously we had observed the westward movement of immature salmon south of Adak Island during July, August and early September, primarily within 50 miles of land. Cruise results showed the abundance centers of salmon to be well beyond 50 miles of the island chain in the western North Pacific Ocean during September and October (Figure 16). The 1-winter-at-sea sockeye salmon (approximately 80% were age 4_3) were abundant just south of Adak at latitude 51°33′N, but farther west they were in greatest abundance near latitude 50°N. Fewer sockeye older than 1-winter-at-sea age were taken; their greatest abundance was also near latitude 50°N.

Chum salmon were distributed differently than the sockeye salmon. Both the 2-year-old fish and the 3- and 4-year-old fish were in greatest abundance at the westernmost stations fished.

Gillnet Dropouts

Four experiments were done to study the loss of fish from high seas gillnets (dropouts). The method of fishing the experimental gillnets was as follows:

8 p.m. Set gear units 1, 2, 3 and 4.
11 p.m. Haul unit 1, remove salmon and reset unit 1.
2 a.m. Haul units 1 and 2, remove salmon and reset unit 2.
5 a.m. Haul units 2 and 3, remove salmon and reset unit 3.
8 a.m. Haul units 3 and 4.

Results of two experiments were unusable because of a combination of weather and tidal current factors affecting the net string and because of difficulty encountered in hauling the gear. The two successful experiments, however, provided data on the time of night fish were caught (8–11 p.m.; 11 p.m.–2 a.m.; 2–5 a.m.; 5–8 a.m.) and on catches in nets fished six, nine and 12 hours compared to the cumulative catches in nets fished for 3-hour periods.

Results of fishing nets at different time-periods during the night indicated that at this season most salmon were taken in the early part of the night (Figure 17). The smallest catches of salmon were taken between the hours of 11 p.m. and 2 a.m., although the catches in set No. 7 were the same for the periods

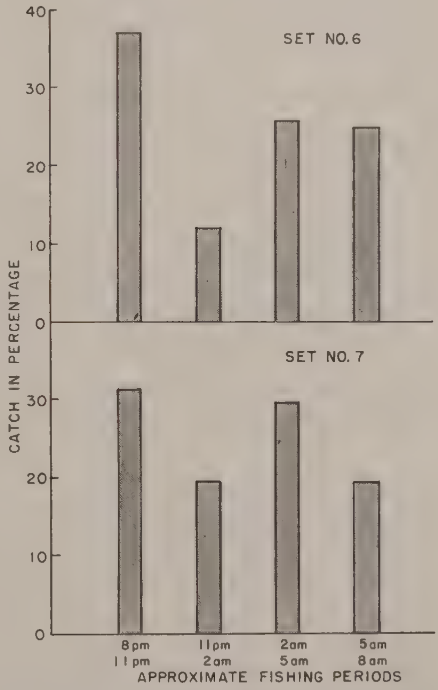

Figure 17. Percentage of total catch by 3-hour time periods.

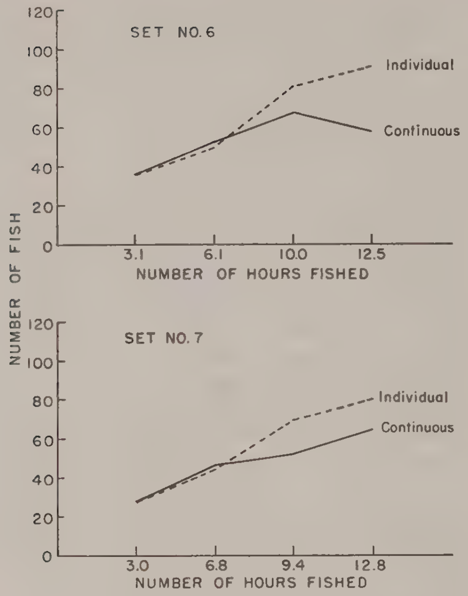

Figure 18. Comparison of the salmon catch in gillnets fished continuously with the cumulative catch in individual nets fished for short intervals during the same time period.

between 11 p.m. and 2 a.m. and between 5 a.m. and 8 a.m.

The catches in gillnet units fished continuously for periods of six, nine and 12 hours and the cumulative catch in individual units fished for 3-hour periods are compared in Figure 18. Less fish were taken in nets fished continuously nine and 12 hours than in the 9- and 12-hour cumulative catches of individual units fished for three 3-hour periods and four 4-hour periods. The catches were similar for the first six hours for the two sets. Thereafter, in both experiments the gear fished continuously caught comparatively fewer fish.

Although the cause of this decrease in catch of the nets fished continuously cannot be specifically deduced from results of these experiments, it is reasonable to hypothesize that the loss is attributable to dropouts. This hypothesis will be more critically tested in future experiments.

Gear Comparisons

Gillnets and longlines were fished simultaneously in sets No. 5 and No. 9 (see Table 10). The 24-shackle gillnet string fished overnight took far more salmon than the 20-skate longline string fished at dawn.

A comparison of the species and age groups in the catches made by gillnets and longlines is given in Table 11. The age composition for both sockeye and chum salmon was similar for the two kinds of gear. Although pink, chinook and coho salmon were represented in gillnet but not in longline catches, their numbers were few.

Lengths of the sockeye and chum salmon caught by the two kinds of gear were similar (Table 12). Sex ratios have not been determined.

Catch data of four longline sets were combined to compare catches of small and large sockeye and chum salmon on the two hook sizes used (Table 13). Although numbers of fish were few, there was no indication that small hooks were selective for 1-winter-at-sea sockeye and 2-year-old chum salmon.

This was in contrast to results of the winter cruise during which the small hooks were apparently selective for 1-winter-at-sea sockeye which averaged about 250 mm in length. The same age group in September and October averaged about 400 mm in length. Presumably, the interim growth increment of 150 mm considerably reduced the selective advantages of small hooks over large hooks during the summer season.

Table 11. Comparison of species and age groups of salmon caught in simultaneous sets of gillnets and longlines, summer cruise, 1964.

Gear	Species and age groups														
	Sockeye				Chum										
	1-winter-at-sea		2-, 3-winter-at-sea		2-year-old		3-, 4-, 5-year-old		Pink		Chinook		Coho		Total
	No.	%	*No.*	%	*No.*	%	*No.*	%	*No.*	%	*No.*	%	*No.*	%	
Gillnets	87	—	59	—	31	—	304	—	1		3		1		486
Gillnets (Adjusted)[1]	174	28.8	59	9.8	62	10.2	304	50.2	1	0.2	3	0.5	2	0.3	605
Longlines	32	21.3	17	11.3	7	4.7	94	62.7	0	0	0	0	0	0	150

[1] Gillnet catches were adjusted to give equal effort on small and large fish since there was unequal effort when fishing gillnets but not when fishing longlines.

TABLE 12. Comparison of fork length distribution and mean sizes of sockeye and chum salmon caught by gillnets and longlines, summer cruise, 1964.

	Sockeye salmon						Chum salmon					
	1-winter-at-sea		2-winter-at-sea		3-winter-at-sea		2-year-old		3-year-old		4-year-old	
Fork length (cm)	GN	LL	GN	LL	GN	LL	GN	LL	GN	LL	GN	LL
33	1	—	—	—	—	—	—	—	—	—	—	—
34	3	2	—	—	—	—	—	—	—	—	—	—
35	4	1	—	—	—	—	3	—	—	—	—	—
36	9	3	—	—	—	—	1	—	—	—	—	—
37	10	—	—	—	—	—	5	3	1	—	—	—
38	9	1	—	—	—	—	8	—	—	—	—	—
39	9	1	—	—	—	—	4	2	—	—	—	—
40	17	6	—	—	—	—	4	1	—	—	—	—
41	11	6	—	—	—	—	—	—	2	3	—	—
42	8	4	—	—	—	—	1	—	2	3	—	—
43	8	4	—	—	—	—	—	1	10	7	—	—
44	5	2	—	—	—	—	—	—	22	19	—	—
45	4	—	—	—	—	—	1	—	35	17	—	—
46	3	—	2	—	—	—	—	—	55	16	—	—
47	—	—	1	—	—	—	—	—	59	12	—	—
48	—	—	1	2	—	—	—	—	44	6	—	—
49	—	—	4	2	—	—	—	—	34	4	1	—
50	—	—	8	4	—	—	—	—	22	2	2	—
51	1	—	9	—	1	—	—	—	14	—	1	—
52	—	—	9	2	—	—	—	—	5	2	1	—
53	—	—	8	2	—	—	—	—	6	—	1	—
54	—	—	4	—	—	—	—	—	5	—	2	—
55	—	—	3	2	—	—	—	—	—	—	3	—
56	—	—	2	—	—	—	—	—	—	—	1	—
57	—	—	—	—	—	—	—	—	—	—	1	—
58	—	—	1	—	—	1	—	—	—	—	4	—
59	—	—	—	—	—	—	—	—	—	—	1	—
60	—	—	—	—	—	—	—	—	—	—	—	—
61	—	—	—	—	—	—	—	—	—	—	1	1
62	—	—	—	—	1	—	—	—	—	—	—	1
Total	102	30	52	14	2	1	27	7	316	91	19	2
Mean fork length (cm)	39.8	40.7	51.6	51.0	—	—	38.3	38.9	47.2	45.5	54.9	—

TABLE 13. Comparison of catches of small and large salmon with small and large hooks, summer cruise, 1964.

SOCKEYE SALMON

Gear	No. of skates	Total catch	1-winter-at-sea	2-, 3-winter-at-sea	Percent 1-winter-at-sea
Small hooks	16	17	13	4	76.5
Large hooks	72	52	34	18	65.4

CHUM SALMON

Gear	No. of skates	Total catch	2-year-old	3-, 4-year-old	Percent 2-year-old
Small hooks	16	27	2	25	7.4
Large hooks	72	90	11	79	12.2

OTHER STUDIES

As subordinate objectives we are analyzing high seas salmon data on visceral adhesions, sub-populations of immatures and distribution in the Gulf of Alaska. Progress on these subjects is summarized under appropriate headings. Detailed reports are forthcoming in separate papers.

Visceral Adhesions in High Seas Salmon

During both the summer cruise of 1963 and the winter cruise of 1964, a substantial percentage of the sockeye salmon examined aboard the *George B. Kelez* were afflicted with multiple visceral adhesions. Frequency of affliction was 9% of the 1963 samples and 26% of the fish examined in 1964. The specimens were characterized by fusion of the tightly compacted visceral mass to the body wall with mesenteric and peritoneal adhesions.

The incidence of adhesions prior to 1963 was recorded during morphological examinations of salmon for racial studies. Less than 1–2% of these sockeye salmon were afflicted with adhesions. The occurrence was rare in chum salmon and was not noted at all in the other salmon species.

Visceral adhesions in sockeye salmon occurred most often in males in their second winter at sea. The majority of these were immature.

Further inquiry into the occurrence and causes of visceral adhesions in salmon is continuing.

Separation of Immature Salmon Sub-Populations by Means of Age Ratios

During the summer field season of 1963, two research vessels, the *George B. Kelez* and the *Bertha Ann*, fished stations south of the Aleutian Chain along longitudes 176°W and 162°W, respectively. The catches from the two sampling areas were compared for age ratios (i.e., $3_1 : 4_2 : 5_3$ and $3_2 : 4_3 : 5_4$ for sockeye salmon and 2- : 3- : 4-year-olds for chum salmon) and direction of travel of the fish.

Preliminary results of comparing age ratios and travel direction indicated that four distinct sub-populations of immature sockeye salmon were encountered. These were the 1-winter-at-sea and 2-winter-at-sea fish in the central Aleutian area and 1-winter-at-sea and 2-winter-at-sea fish in the western Gulf of Alaska. The two western groups of sockeye salmon moved west out of the sampling area by late August and were replaced by two bodies of fish from the western Gulf of Alaska. The latter two sub-populations remained dominant over the entire eastern North Pacific into September.

Analyses of age ratios of chum salmon showed sub-populations apparently existed in the central Aleutian area and western Gulf of Alaska. Their migration patterns, however, were not clear compared to the sockeye salmon. Analyses of sub-population differences are continuing.

Salmon Distribution in the Gulf of Alaska

The main features of a study of salmon distribution in the Gulf of Alaska include: (1) the separation in the spring season of maturing and immature salmon; (2) the change in mid-summer of catches of predominantly maturing sockeye and chum salmon to catches of immature fish; (3) the large abundance of salmon in the western part of the Gulf of Alaska; and (4) the scarcity of immature salmon having spent at least one winter at sea in the eastern part of the Gulf in late summer.

SUMMARY

In a winter fishing cruise (January 17-March 18, 1964), planned jointly with Canada, longline gear took pink salmon or steelhead, or both, at stations 360 to 900 miles off the U.S. coast at about latitude 46°-30′N. Sockeye salmon constituted the only species (with the exception of one small chum salmon taken in a gillnet set) taken at stations in the Aleutian area, both in the North Pacific Ocean and Bering Sea. Sockeye salmon were more abundant in the North Pacific Ocean than in the Bering Sea.

Younger age groups of sockeye salmon decreased to the west and to the north in areas where sockeye were caught, between longitudes 165°W and 175°E and between latitudes 49°N and 57°N. Sockeye salmon which had spent one and two winters at sea appeared to be smaller in length in 1964 when compared with fish of the same age groups captured in 1962 and 1963; 3-winter-at-sea fish were comparable for the three years. Bering Sea sockeye salmon were larger in average length than sockeye taken in the North Pacific Ocean. Winter pink salmon were from 225 mm to 390 mm in size. Most of the steelhead caught were in their first winter at sea.

The majority of the female sockeye examined by serological methods showed onset of maturation; these fish were divided about equally between ages 4_2, 5_3, 5_2 and 6_3. A few fish, ages 4_2 and 5_3, did not indicate onset of maturation.

Comparative catch data of longlines and gillnets during the winter cruise indicated that gillnets took more small fish than the longline gear. In longline sets employing both large and small hook sizes, the smaller hooks were selective for small sockeye salmon.

During the late summer cruise in the western North Pacific, 1-winter-at-sea sockeye and 3-year-old chum salmon dominated the catches. Sockeye salmon were in greatest abundance at stations along longitude 173°E, while chum salmon apparently were in greatest abundance at stations along longitude 169°E.

Experiments concerned with loss of fish from gillnets were undertaken in September and October. Most fish were captured between the hours of 8 p.m. and 11 p.m. The smallest catches were made between the hours of 11 p.m. and 2 a.m. The catches of gillnets fished continuously beyond six hours were smaller than the cumulative catches of nets fished for shorter time periods.

In simultaneous fishing experiments of gillnets and longlines during the summer, we noted that a 24-shackle gillnet string caught many more salmon than a 20-skate longline string. Age compositions for both sockeye and chum salmon were similar for the two kinds of gear. Lengths of sockeye and chum salmon caught by the two kinds of gear were also similar. Other salmon species (one pink, three chinook and one coho) were taken only in gillnets.

Apparently, small longline hooks were not selective for small sockeye and chum salmon during the late summer fishing cruise.

Visceral adhesions in sockeye salmon were noted in 9% of the samples examined during the 1963 summer cruise and in 26% of the fish examined during the 1964 winter cruise. These percentages were substantially greater than were recorded in past seasons' samples.

Preliminary results of comparing salmon catches, in terms of age ratios, of two sampling areas in 1963 indicated that four distinct sub-populations of immature sockeye salmon were encountered: 1- and 2-winter-at-sea fish in the central Aleutian area and 1- and 2-winter-at-sea fish in the western Gulf of Alaska.

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OCEANOGRAPHY

by F. Favorite

During the past several years, we have shown that the major oceanographic features of the Subarctic Pacific Region are relatively permanent. In order to more clearly define the water properties and the circulation, we have commenced detailed chemical and biological studies and have experimented with drifting radio buoys. Last year most of our research was devoted to the installation and testing of new equipment and to the development of techniques.

Outfitting the *George B. Kelez* for oceanographic work has been time-consuming, but has relieved us of many of the difficulties associated with modifications and temporary installations when working from chartered vessels. Most of the testing of equipment and techniques has been accomplished in local waters during short periods scheduled between long fishing cruises in Aleutian waters (Figure 19).

Biological and chemical studies have been concerned with the availability of organisms which constitute the food of salmon, and with the chemical nutrients and lower trophic levels associated with production in these organisms. Two important variables which may limit production in phytoplankton are supply of chemical nutrients and extensive grazing by higher trophic levels. In addition to the commonly measured chemical nutrients—silicates, phosphates and nitrates—there are both elemental and complex substances present in the sea in trace amounts which are necessary for survival and growth of phytoplankton. Variation in the relative concentration of these micronutrients may be a limiting condition in production by various phytoplankton organisms.

We are improving our present chemical techniques and are attempting to develop new techniques for the measurement of trace elements in the marine environment. Acquisition of a light absorption spectrophotometer has made it possible to refine our techniques for the measurement of chlorophyll and to devise a modification of the Winkler method for the determination of low levels of dissolved oxygen using an ab-

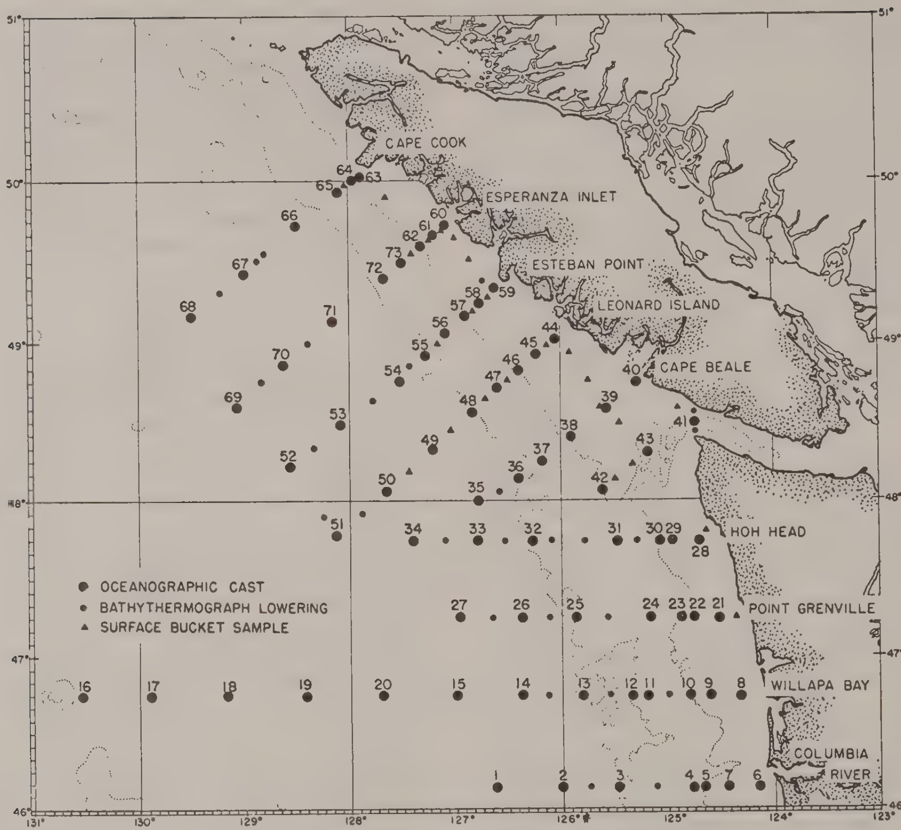
CAPE COOK
ESPERANZA INLET
ESTEBAN POINT
LEONARD ISLAND
CAPE BEALE
HOH HEAD
POINT GRENVILLE
WILLAPA BAY
COLUMBIA RIVER
● OCEANOGRAPHIC CAST
• BATHYTHERMOGRAPH LOWERING
▲ SURFACE BUCKET SAMPLE
51°
50°
49°
48°
47°
46°
131°
130°
129°
128°
127°
126°
125°
124°
123°

FIGURE 19. Oceanographic stations—October and November 1963.

sorptiometric measurement of the iodine-chloroform complex developed by solvent extraction of the treated sea-water samples. An absorptiometric method has been developed for the simultaneous routine determination of particulate aluminum and iron in sea water. Using this technique, we have shown that the freshwater plume off the mouth of the Columbia River is as well defined by the distribution of particulate aluminum (Figure 20) as it is by the distribution of salinity (Joyner, 1964). Techniques for analyses of other trace elements, such as zinc, copper, nickel and manganese are being developed utilizing an atomic absorption spectrophotometer. These studies are designed to improve our understanding of the chemistry of the salmon environment and should provide additional indicators of the location and extent of discrete water masses that may influence movements of salmon.

During this year we have also begun studies of production and the composition of the autotrophic plankton. Shipboard and laboratory capabilities were developed to sample and analyze sea water for plankton pigment content and species of phytoplankton. Samples were collected from levels of 100, 56, 23, and two percent of the surface light intensity. *In situ* intensity was measured by an irradiance meter (Marine Adviser, Model C-la). Collection of the phytoplankton and analysis of pigment have been successful, but further refinements in technique are needed in measuring the *in situ* light intensity.

The inadequacy of present sampling techniques is one of the principal difficulties encountered in an investigation of the availability of organisms which serve as food for salmon. The vast fishery resources in the Subarctic Pacific require an enormous amount of zooplankton to sustain them. Our earlier efforts at sampling zooplankton in this region involved vertical hauls from 150 meters to the surface with

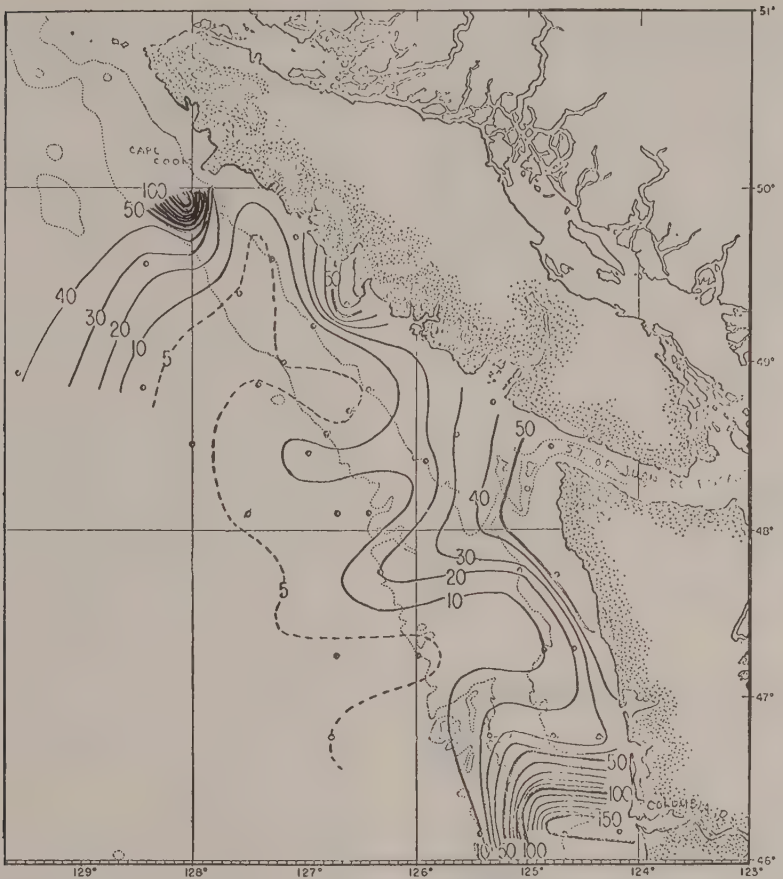

FIGURE 20. Distribution of particulate aluminum at the surface in coastal waters of the Pacific Northwest—spring 1963. Contours in μg-at Al/L × 10^{-2}.

½-meter, No. 6 mesh plankton nets. The composition of these samples was not representative of the organisms found in salmon stomachs, and extrapolations of the density in the sea of the few food organisms found in the samples produced obvious underestimates.

Realizing the inadequacy of the vertical hauls, we instigated use of a modified 3-foot Isaacs-Kidd trawl. The device captures many of the larger plankton forms, but is ineffective in capturing the small nekton and squid which we have found to be of major importance in the salmon diet during winter. Experiments with the Isaacs-Kidd trawl have shown the vertical distribution of organisms to be complex and to vary from area to area. During 1961, we used the trawl at seven different locations to sample the water column at 25-meter intervals to a depth of 200 meters for a 24-hour period. Three representative stations are shown in Figure 21 ; two are located south of the Aleutian Island area and one in the central Bering Sea. Maximum concentrations of biomass at these three stations occurred at 50, 125 and 125 meters during the day, and at 25, 25, and 100 meters during the night (Figure 22). Of particular significance is the fact that maximum biomass during day or night in the central Bering Sea (Station 3) was found at or below 100 meters. In this area, we have obtained large gillnet catches of sockeye salmon only near the Bristol Bay shelf, even though tagging experiments show that the salmon move eastward through the central Bering Sea.

We have interpreted these data to mean that incidental or superficial plankton sampling, with

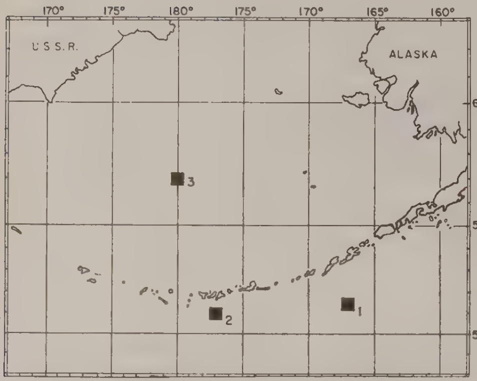

Figure 21. Locations of special zooplankton sampling stations.

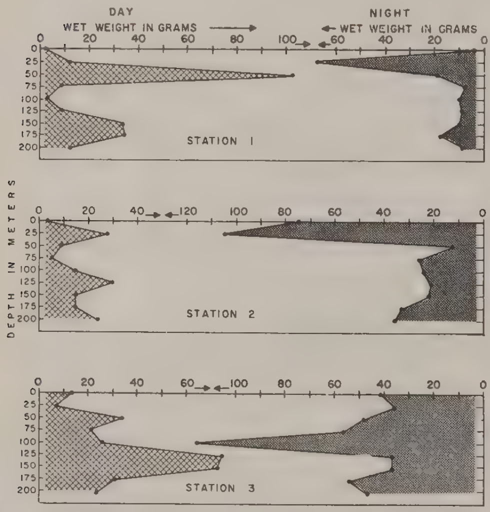

Figure 22. Wet weights in grams of the biomass obtained during day and night at 25-meter depth intervals using a 3-foot modified Isaacs-Kidd trawl.

devices other than closing nets which permit uncontaminated sampling at discrete depths and possess a known capability to capture specific organisms, will not increase our knowledge of the availability of food organisms. During the past year, we experimented with a 6-foot trawl equipped with a pressure device which individually opened and closed three nets at depths selected as optimum after investigation of the water structure and sonic traces. The pressure device was not sufficiently sensitive to sample the shallow surface layer which exists in the Subarctic Region and, before modifications could be made, the trawl was lost at sea. We are making test arrangements at the present time for a similar discrete-depth sampler equipped with multiple nets capable of being electronically and remotely opened and closed.

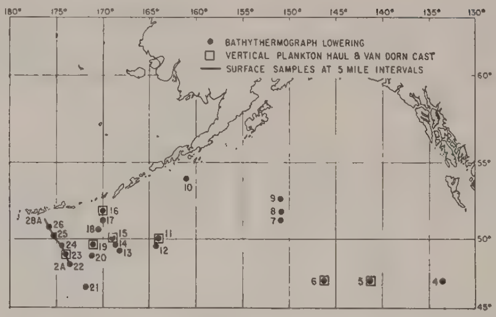
180°
175°
170°
165°
160°
155°
150°
145°
140°
135°
130°
● BATHYTHERMOGRAPH LOWERING
☐ VERTICAL PLANKTON HAUL & VAN DORN CAST
— SURFACE SAMPLES AT 5 MILE INTERVALS
60°
55°
50°
45°
1
2A
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
28A

Figure 23. Locations of oceanographic observations during a joint cruise of the *G.B. Reed* and the *George B. Kelez.*

During January and February, we participated in a joint fishing-oceanographic cruise of the *George B. Kelez* (Bureau of Commercial Fisheries Biological Laboratory, Seattle, Washington) and the *G. B. Reed* (Fisheries Research Board of Canada Biological Station, Nanaimo, B.C.). Locations of observations made aboard the *Kelez* are shown in Figure 23. Vertical plankton hauls were made using a net provided by the *G. B. Reed* and samples were forwarded to Nanaimo for analysis. Samples from the Van Dorn casts were analyzed at Seattle for phytoplankton pigments and species.

Even with the background environmental knowledge provided by Dodimead, Favorite and Hirano (1963), optimum selection of fishing locations will require knowledge of oceanographic conditions existing over a large area at the time of the cruise. This knowledge can be acquired in two ways. First, salmon distribution studies may be coordinated with large-scale oceanographic cruises. This requires advance planning. The scope of various investigations and the time required for analysis and integration of results prevents conducting coordinated cruises as frequently as those devoted exclusively to fishing. The coordinated cruises, however, serve the necessary function of integrating the fragmentary pieces of knowledge into a unified picture. A proposal to conduct a coordinated oceanographic investigation across the North Pacific Ocean during 1966 has been made to the U.S. National Science Foundation.[1]

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[1] U.S.-Japan Cooperative Science Programs (n.d.) Joint Report of the Planning Meeting in Physical Oceanography. 26 p. (Processed.)

A second method of ascertaining environmental conditions prior to fishing cruises would be to obtain data from moored or drifting buoys. There are at least one Soviet and one U.S. proposal to establish a network of moored buoys in the North Pacific Ocean. As indicated in Favorite and Morse (1963), these buoys would permit more accurate forecasts of surface conditions in the Pacific. Moored buoys, however, would not necessarily be as useful as drifting buoys to denote circulation and locations of fronts or gyres, which are of particular interest to fishing investigations.

During May 1964, we conducted an experiment with three drifting, transponding, telemetry buoys off the Washington Coast. One of the buoys was in the water over two months, drifted over 300 miles and was recovered in good condition. Although the buoys were purchased for use in conjunction with other programs, we hope to prove their effectiveness in monitoring conditions in the salmon environment across the Pacific Ocean. Using a frequency of 4134.5 kc, we were able to interrogate and hear the transponding signal from a buoy released off the Washington Coast, not only from our laboratory in Seattle, but also from the *Kelez*, which was in the Gulf of Alaska (Figure 24). When experiments with these buoys are completed, we expect to achieve transmission ranges of over 1,200 miles and to record and receive temperature data from the surface to a depth of 300 meters. Radio stations near Hakodate, Adak and Seattle (Figure 25) would provide an adequate network of stations to interrogate and receive data from buoys. Optimum utilization of current patterns in Subarctic waters would be obtained by releasing buoys at periodic intervals in the vicinity of the Kuril Islands. Frequent determination of the position of the buoys by use of aircraft, ships, and eventually even by satellite, would provide sufficient knowledge of conditions and currents to show average and anomalous temperatures and circulation patterns in the salmon environment that could be investigated by subsequent salmon fishing cruises.

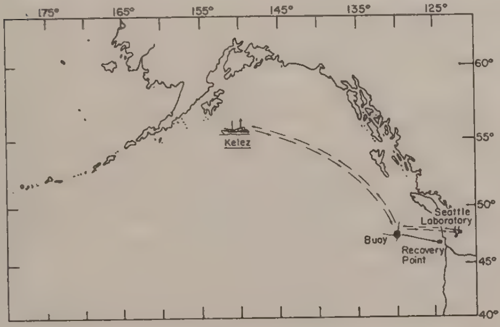

Figure 24. First test of a drifting, transponding telemetry buoy in the Pacific Ocean.

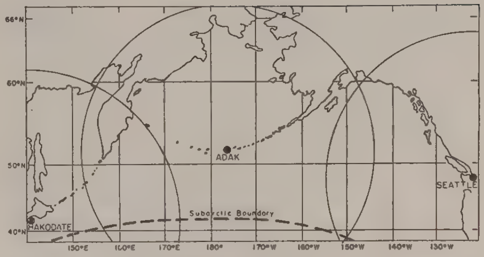

Figure 25. Approximate areas in which data transmitted from radio buoys having a range of 1,200 miles could be received at Hakodate, Adak and Seattle.

These are the equipment and the techniques we are presently devising and testing, and these are the directions in which we believe that oceanographic research should proceed if we are to ascertain eventually why, and in what manner, the salmon respond to the marine environment.

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OCEAN MORTALITY AND GROWTH

by R.H. Lander, G.K. Tanonaka,
K.N. Thorson and T.A. Dark

Parker (1960; 1963), Taguchi (1961a; 1961b), Ricker (1962; 1964), Doi (1962), Fredin (1963) and Hirschhorn (MS 1964) have reported on mortality and growth estimates and on the problem of estimating maximum sustainable yields in certain North American and Asian stocks of chinook, chum, pink and sockeye salmon. A common purpose of these authors was to assess the effects upon yield of exploiting Pacific salmon before they reach coastal waters in the terminal marine stages of their spawning migrations.

The most general approach to assessing the potential yield from a given number of recruits in salmon populations is to determine and evaluate the resultant of growth and mortality estimated for the entire ocean life. On occasion it is not only of interest, but necessary, to ascertain the increment or decrement in potential yield during a specific stanza of life history. One method is to prorate the resultant of total ocean growth and mortality to the interval of interest. We have adopted the alternate approach of obtaining direct estimates by comparing the differences between growth over mortality between two specific points in time. Initially, using tagging methods and theory, we will assess the feasibility of estimating rates of mortality between two points in time during the final two months of ocean life. Growth rates will be obtained concurrently.

To define operational problems in investigating the terminal ocean mortality of maturing Bristol Bay sockeye in June 1964, an exploratory tagging study was conducted east of 175°W in the Bering Sea.

To provide a basis for evaluating growth rates, we have analyzed morphometric data from sockeye, chum, pink and coho salmon taken in gillnets on the high seas in 1955 through 1962.

MORTALITY

Figure 26 shows positions fished by the *George B. Kelez* in June 1964. The irregular station pattern reflects unsuccessful efforts to locate or catch large numbers of migrating fish for tagging with a single vessel. The catches are shown in Table 14.

In an effort to decide whether poor fishing was due to low density of maturing Bristol Bay sockeye or to their failure to take salted anchovy baits, gillnets were fished with longlines at seven of our 16 stations (Table 14). For these seven stations, data were obtained by setting gillnets at dawn, putting out longlines nearby, hauling gillnets, and finally retrieving longlines. The difference between median clock

TABLE 14. Catch, release and recovery data from 1964 ocean

Stn. no.	Date	Location		Gear	No. of units fished[1]	No. caught (tagged)				
		Lat.	Long.			Sockeye	Chum	Pink	Chinook	Total
1	6/12	55°00′N	174°50′W	LL	20	3(3)	3(1)	12(7)	2(1)	20(12)
2	6/12	53°35′N	173°53′W	LL	20	3(2)	3(1)	0	0	6(3)
3	6/14	52°50′N	173°35′W	LL	20	2(2)	8(7)	3(2)	10(4)	23(15)
4	6/15	55°40′N	172°24′W	LL	5	1(1)	2(2)	0	2(2)	5(5)
5	6/16	53°35′N	173°53′W	LL	5	0	2(1)	4(1)	1(1)	7(3)
6	6/17	53°38′N	168°15′W	LL	10	0	0	0	0	0
7	6/18	54°45′N	165°00′W	LL	10	7(4)	3	3	0	13(4)
				GN	6	12	17	0	0	29
8	6/19	56°29′N	170°12′W	LL	20	18(14)	3(3)	1	0	22(17)
9	6/20	56°41′N	169°55′W	LL	20	19(12)	6(3)	0	0	25(15)
10	6/21	55°17′N	166°54′W	LL	18	18(11)	4(1)	1(1)	0	23(13)
				GN	6	16	2	0	0	18
11	6/23	55°15′N	164°00′W	LL	20	1(1)	0	0	2	3(1)
12	6/24	56°30′N	160°20′W	LL	15	22(19)	2(2)	0	0	24(21)
				GN	9	16	2	0	0	18
13	6/25	57°30′N	161°07′W	LL	18	20(15)	31(27)	0	0	51(42)
				GN	9	45	12	0	0	57
14	6/26	58°26′N	161°52′W	LL	18	0	1	0	0	1
				GN	9	1	7	0	0	8
15	6/27	57°06′N	158°54′W	LL	17	43(37)	0	0	0	43(37)
				GN	9	103	0	0	0	103
16	6/28	57°44′N	159°24′W	LL	18	10(8)	6(4)	0	1(1)	17(13)
				GN	9	40	12	0	0	52
Totals						400(129)	126(52)	24(11)	18(9)	568(201)

[1] LL = Number of skates of longline
GN = Number of shackles of gillnet

[2] S = sockeye
C = chum
P = pink

times of hauling and setting was taken as the measure of effective fishing time; average fishing times for all seven stations were 2.75 hours and 1.51 hours for gillnets and longlines, respectively. Adjustment of individual catches in Table 14 to unit time and effort (not shown here) still leaves the cause of poor fishing in doubt.

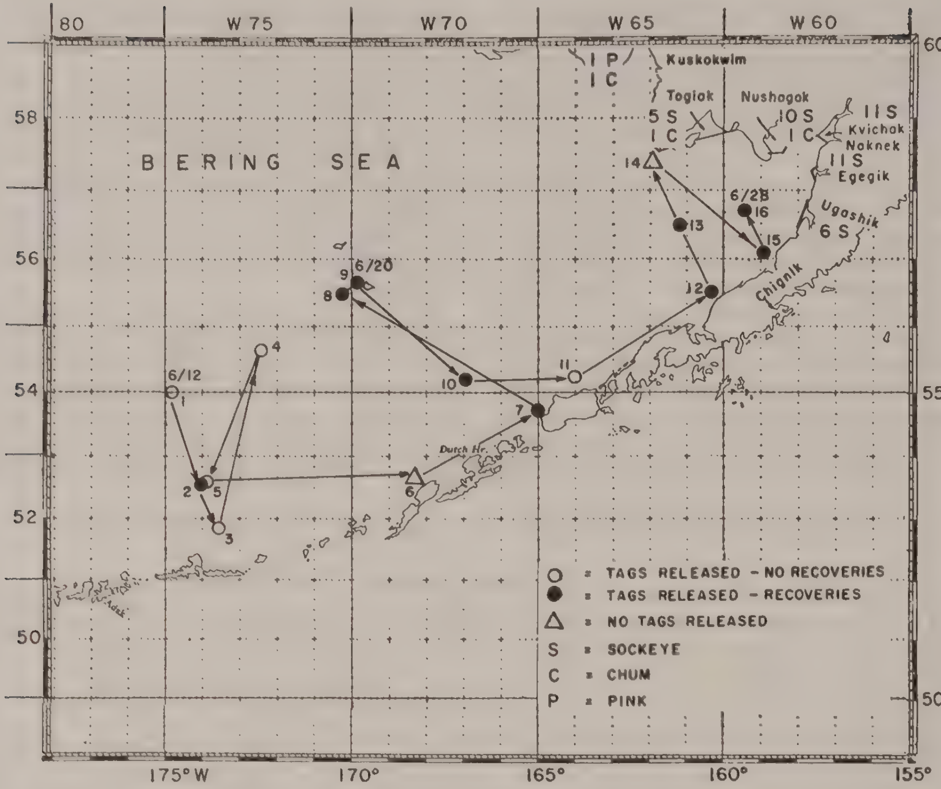
Our catches may have reflected the low return of sockeye to Bristol Bay in 1964. In 1960 and 1961, however, the catches by Japanese research vessels fishing longlines in the eastern Bering Sea were generally poor despite very high returns to Bristol Bay (International North Pacific Fisheries Commission, 1961 and 1963). Our own low catches by longline cannot be attributed to cessation of feeding, for large volumes of zooplankton and small fish were found in the stomachs of untagged sockeye taken as close to the Bristol Bay fishery as Station 15 (Figure 26). Although there is no analytical basis for interpretation, longlines of the type used by the Japanese and United States research vessels are evidently rather inefficient for catching maturing Bristol Bay sockeye in the eastern Bering Sea.

We tagged only fish taken on longlines and released only those without apparent disability. The recovery phase was conducted with the cooperation of Bristol Bay fishermen and cannery personnel and the Fisheries Research Institute of the University of Washington, which also supplied the disc tags used. Catches and recoveries were too few to warrant detailed analysis at this time.

To avoid the potential problems of selectivity of disc-tagged fish by gillnets and of tag reportability in future work, we explored the possibility of installing in Bristol Bay canneries certain detection apparatus for an internal, color-coded, magnetic wire tag (Jefferts *et al.*, 1963). Mr. P. K. Bergman of the State of Washington Department of Fisheries conducted

mortality experiment on maturing Bristol Bay sockeye.

Inshore tag recoveries by area and species[2)]						High seas recoveries by INPFC area (2°×5°)				
Naknek-Kvichak	Egegik	Ugashik	Togiak	Nushagak	Kuskokwim	E7058	E7558	E7560	Total	Recovery rate (%)
0	0	0	0	0	0	1 (P)	0	0	1 (P)	8.3
1 (S)	0	0	0	0	0	0	0	0	1 (S)	33.3
0	0	0	0	0	1 (P)	1 (P)	2 (C)	0	2 (P), 2 (C)	26.7
0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0
0	1 (S)	0	0	0	0	0	0	0	1 (S)	25.0
0	0	0	0	0	0	0	0	0	0	0
1 (S)	1 (S)	0	2 (S)	0	0	0	0	0	4 (S)	23.5
2 (S)	1 (S)	0	0	1 (S)	0	0	0	1 (C)	4 (S), 1 (C)	33.3
1 (S)	2 (S)	1 (S)	0	0	0	0	0	0	4 (S)	30.8
0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0
1 (S)	1 (S)	2 (S)	0	2 (S), 1 (C)	0	0	0	0	6 (S), 1 (C)	33.3
0	0	0	0	0	0	0	0	0	0	0
2 (S)	0	0	2 (S), 1 (C)	2 (S), 1 (C)	4 (C)	0	0	0	7 (S), 6 (C)	31.0
0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0
2 (S)	4 (S)	3 (S)	1 (S)	2 (S)	0	0	0	0	11 (S)	29.7
0	0	0	0	0	0	0	0	0	0	0
3 (S)	1 (S)	0	0	2 (S)	0	0	0	0	7 (S)	53.8
0	0	0	0	0	0	0	0	0	0	0
13 (S)	11 (S)	6 (S)	5 (S) 1 (C)	10 (S) 2 (C)	4 (C) 1 (P)	2 (P)	2 (C)	1 (C)	45(S), (10C) 3 (P)	28.8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BERING SEA
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Kuskokwim
Togiok
5 S
1 C
Nushagok
10 S
1 C
11 S
Kvichok
Noknek
11 S
Egegik
Ugashik
6 S
Chignik
Dutch Hr.
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13
14
15
16
○ = TAGS RELEASED – NO RECOVERIES
● = TAGS RELEASED – RECOVERIES
△ = NO TAGS RELEASED
S = SOCKEYE
C = CHUM
P = PINK

FIGURE 26. June tagging stations of the *George B. Kelez* with numbers of salmon recovered shown by inshore area and species.

this survey. Installations would be too expensive at present levels of research effort, because of the nature of the equipment, the number of canneries and the differences in methods of handling fish.

The expectation of returns from high seas tagging has been demonstrated to be comparatively low. In order to minimize the loss of fish from the immediately harmful effects of tagging, and also to gain insight into latent effects, we have commenced physiological studies. The present objective is to define and counteract the specific causes of physiological stress associated with tagging. These studies will be continued during the tagging experiments in June and July, 1965.

Growth

Lengths and weights of 48,756 specimens taken in June and July (1955–1962) were analyzed for ocean growth of sockeye, chum, pink and coho salmon (Table 15). About 80% of these were taken by U.S. research vessels which fished gillnets of graduated mesh sizes. Japanese research and commercial vessels and Canadian research vessels accounted for the remainder. In high seas sampling the best representation of age and maturity groups was obtained during June and July. Therefore, July 1, the midpoint of this interval, was chosen as the point to which all mean lengths and weights were referred.

In Table 15, the estimated mean sizes on July 1 for sockeye, chum, pink and coho salmon are summarized by ocean age and maturity. The original measurements for all species but coho were obtained from frozen specimens. Lander and Tanonaka (1964) computed factors for converting lengths and weights of frozen fish to a fresh basis for sockeye salmon. Assuming these conversion factors to be applicable to chum and pink salmon, all data in Table 15 are expressed as fresh fish lengths and weights. For coho salmon, fresh lengths were those obtained aboard U.S. research vessels, while fresh weights were those

TABLE 15. Estimated mean fork lengths and body weights, by ocean age and maturity, of sockeye, chum, pink and coho salmon on July 1[1].

Species	Maturity[2]	Age (winters at sea)	Sample size	Length (mm)	Weight (dkg)
Sockeye	Immature	1	900	339	45
		2	2,392	479	128
		3	200	526	173
		Sub-total	*3,492*		
	Maturing	1	7	400	80
		2	4,978	534	195
		3	3,201	580	251
		4	148	596	272
		Sub-total	*8,334*		
		Total sockeye	*11,826*		
Chum	Immature	1	3,055	342	46
		2	5,732	473	115
		3	4,115	516	160
		4	274	542	180
		5	8	554	185
		Sub-total	*13,184*		
	Maturing	2	992	538	198
		3	5,734	565	224
		4	1,559	581	242
		5	100	588	250
		Sub-total	*8,385*		
		Total chum	*21,569*		
Pink	Maturing	1	12,649	480	138
		Total pink	*12,649*		
Coho	Maturing (U. S.)	1	2,450	558	—
	(Japan)	1	262	—	240
		Total coho	*2,712*		
		TOTAL, ALL SPECIES	48,756		

[1] Collected in 1955 through 1962.

[2] Gonad weight 2 g and less = immature male: gonad weight 15 g and less = immature female. All pink and coho assumed to be maturing from evidence of age and size.

recorded aboard Japanese commercial vessels in 1960 (Japan-Soviet Fishery Commission, 1961).

Lander and Tanonaka (1964) also showed for sockeye salmon that mesh selectivity does not seriously bias an estimate of the actual length composition providing the catches are from all mesh sizes in a graduated series. Therefore, the data in Table 15 further assume no serious bias in estimates of size composition for pink, chum and coho salmon.

Figures 27 and 28 show the estimated mean lengths and weights, respectively, of fresh fish as listed in Table 15. The connecting lines indicate related stages, not known or presumed patterns of seasonal growth; extension of these lines beyond July 1 reminds the reader that spawning may occur later than July 1.

Figure 27 shows that the weight of maturing coho is much greater than that of maturing pink or sockeye after one winter at sea. By July 1, after two winters at sea, immature sockeye slightly exceed immature chum in weight—a situation which prevails thereafter for maturing fish as well. Immatures weigh less than maturing fish at a given ocean age, and the rate of increase in weight of immatures diminishes after one winter at sea.

Figure 28 shows a similar pattern of annual changes in length. Here, however, the increment during the first year at sea is nearly as large for pink as for coho salmon. For all species, the greatest annual increment in length evidently occurs during the first year.

Growth studies to date have been based on successive sampling of one or more stocks on the high seas. A study of pink salmon growth from tagging records is in progress. We plan to (1) procure additional data on sizes of Pacific salmon between their entry to salt water and their escapement to the spawning grounds; (2) assess, as practicable from separate studies, time-independent sources of variation; and (3) construct mathematical models of long- and short-term growth for use in yield equations.

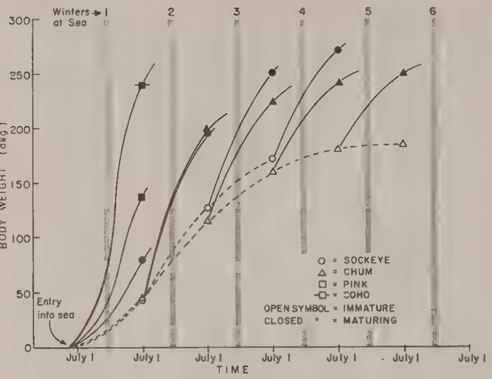

FIGURE 27. Estimated mean body weights on July 1 of sockeye, chum, pink and coho salmon. Connecting lines indicate related stages, not actual patterns of growth. Average weight at time of entry into the marine environment were determined from compilations or observations cited in the following sources: Disler (1953), Levanidova (1957), Piskunov (1955), Ricker (1962), Soin (1954) and Synkova (1951).

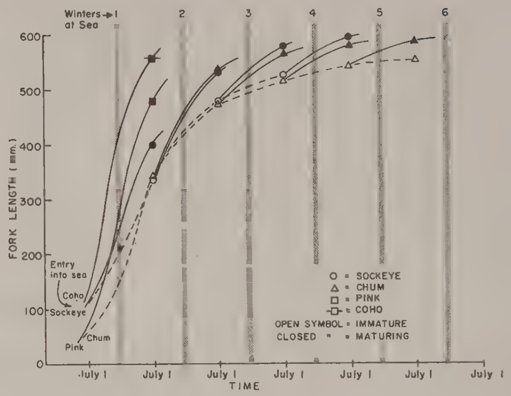

FIGURE 28. Estimated mean fork lengths on July 1 of sockeye, chum, pink and coho salmon. Connecting lines indicate related stages, not actual patterns of growth. Average length at time of entry into the marine environment were determined from compilations or observations cited in the following sources: Disler (1953), Levanidova (1957), Piskunov (1955), Ricker (1962), Soin (1954) and Synkova (1951).

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TABLE 16. Reactions of 1964 North American sockeye salmon

Reagent:	96			101			259			261		
Area:	Total sample	No. positive	Percent positive	Total sample	No. positive	Percent positive	Total sample	No. positive	Percent positive	Total sample	No. positive	Percent positive
Wood R.	24	3	13	24	4	17	24	10	42	24	20	83
Kvichak	26	12	46	26	6	23	26	6	23	26	25	96
Branch	24	2	8	24	0	0	24	1	4	24	11	46
Naknek	26	11	42	26	10	39	26	7	27	26	23	88
Egegik	24	3	13	24	5	21	24	5	21	24	17	71
Karluk	25	5	20	25	1	4	25	4	16	25	14	56
Kenai[1)]	25	9	36	25	0	0	25	5	20	25	17	68
Kenai[2)]	21	4	19	21	7	33	21	2	10	21	13	62
Copper R.	50	20	41	50	7	14	50	7	14	50	35	70
Skeena	48	42	88	48	8	17	48	6	13	48	32	67
Cultus Lake	25	18	72	25	8	32	25	3	12	25	19	76
Chi-square results		89.9**			22.6*			17.8			26.2**	

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SALMON SEROLOGY

by Fred M. Utter and Warren E. Ames

Serological research has as its primary objective the differentiation of Asiatic and American stocks of Pacific salmon. Other objectives include serological separation of major American stocks which may intermingle on the high seas and a serological approach to problems pertinent to the Commission. Currently, the major emphasis in our work is concerned with blood grouping, using rainbow trout isoimmune sera.

erythrocytes using 16 rainbow trout isoimmune sera.

268			269			276			277		
Total sample	No. positive	Percent positive	Total sample	No. positive	Percent positive	Total sample	No. positive	Percent positive	Total sample	No. positive	Percent positive
24	7	29	24	4	17	24	21	88	24	10	42
26	5	19	26	1	4	26	24	92	26	19	73
24	6	25	24	2	8	24	11	46	—	—	—
26	11	42	26	3	12	26	24	92	26	13	50
24	6	25	24	10	42	24	23	96	24	8	33
25	6	24	25	3	12	25	19	76	25	16	64
25	7	28	25	0	0	25	23	92	25	11	44
21	5	24	—	—	—	21	15	71	21	6	29
50	11	22	50	18	36	50	34	68	50	35	70
24	1	4	48	8	17	48	26	54	48	34	71
25	6	24	25	19	76	25	13	52	25	13	52
	11.0			70.9**			48.2**			27.4**	

Continued . . .

Table 16.

Reagent:	282			287			289			291		
Area	Total sample	No. positive	Percent positive	Total sample	No. positive	Percent positive	Total sample	No. positive	Percent positive	Total sample	No. positive	Percent positive
Wood R.	24	6	25	24	10	42	—	—	—	24	3	13
Kvichak	26	2	8	26	6	23	26	18	69	26	8	31
Branch	24	1	4	24	7	29	24	10	42	24	3	13
Naknek	26	3	2	26	14	54	—	—	—	26	3	12
Egegik	24	5	21	24	8	33	—	—	—	24	10	42
Karluk	25	5	20	25	8	32	25	11	44	25	3	9
Kenai1)	25	0	0	25	14	56	25	17	68	25	12	48
Kenai2)	21	8	38	21	8	38	—	—	—	21	17	81
Copper R.	50	7	14	50	21	42	50	30	60	—	—	—
Skeena	48	8	17	48	12	25	48	23	48	48	4	8
Cultus Lake	25	21	84	25	6	24	—	—	—	13	6	46
Chi-square results		79.1**			15.9			8.4			64.4**	

* Significant at the 5% level.

** Significant at the 1% level.

1) Sample collected July 20, 1964.

2) Sample collected August 10, 1964.

Research on Sockeye Cell Antigens

Rainbow trout isoimmune sera have proved to be very effective in detecting individual differences in Pacific salmon species, particularly in sockeye salmon. On the basis of extensive blood group work done with higher vertebrates and the evidence we have obtained from rainbow trout data, there is little doubt that the individual variations detected by rainbow trout isoimmune sera reflect individual genetic variations. A factor complicating the use of these isoimmune reagents is the frequent presence of more than one serological specificity in a given reagent. This has been minimized or eliminated by the use of absorption techniques or by diluting out weaker specificities. Through selective matings and immunizations, we are progressing toward more refined reagents without the necessity of absorption or dilution.

Sixteen reagents were selected for testing of the 1964 sockeye salmon samples. Most of these reagents had demonstrated significant heterogeneity between Bristol Bay areas in the 1963 samples. The samples collected in 1964 were from a number of North American areas in addition to Bristol Bay. Reaction frequencies and between-area chi-square tests for the 1964 sockeye samples tested with selected rainbow trout isoimmune reagents are presented in Table 16. Most of the reagents detected significant differences in frequencies between areas, and there appears to be the possibility of separation of certain areas by the use of some of the reagents either alone or in combination with other reagents. A particularly interesting frequency pattern occurred with reagent 96. The frequency of reaction from the two most southern areas was considerably higher than that of the other areas. Although certain reagents did not demonstrate significant heterogeneity between the areas sampled, they may be capable of discrimination of other stocks, including those of Asiatic origin.

A limited number of pink and chum salmon samples were taken and screened for ability to react with a large number of rainbow trout isoimmune sera. While these species did not appear to cross-react with the isoimmune reagents as extensively as sockeye salmon, certain reagents were found which detected individual differences in both species.

Table 17 compares reactive frequencies of chum salmon erythrocytes from two Puget Sound areas, using five reagents. Significant differences between areas were observed for three reagents. Table 18 compares reactive frequencies of pink salmon erythrocytes from four areas in Alaska and British Columbia using four reagents. Two of the reagents detected statistically significant differences between areas. Of particular interest are the frequency differences for reagents 504 and 511 between the adjacent Metlakatla and Skeena areas, indicating that these stocks may be capable of separation by serological means.

Studies on Serum Antigens

Although major emphasis has currently been placed on blood grouping work, serum was collected from most of the blood samples taken during the past year.

Continued.

295			3127			3128			3167		
Total sample	No. positive	Percent positive	Total sample	No. positive	Percent positive	Total sample	No. positive	Percent positive	Total sample	No. positive	Percent positive
24	4	17	24	9	38	24	1	4	24	0	0
26	17	65	26	17	65	26	0	0	26	3	12
24	7	29	24	8	33	24	0	0	24	5	21
26	21	81	26	7	27	26	2	8	26	0	0
24	17	71	—	—	—	24	19	79	24	16	67
25	15	60	25	7	28	25	0	0	25	14	56
25	19	76	25	12	48	25	0	0	25	16	64
21	11	52	—	—	—	21	0	0	—	—	—
50	34	68	50	31	62	—	-	—	—	—	—
48	24	50	48	29	60	—	—	—	24	24	100
—	—	—	18	3	17	25	0	0	—	—	—
	40.0**			28.7**			144.2**			98.4**	

Sockeye salmon samples were tested by double diffusion analysis for the presence of the " H " and " C " factors. The occurrence of both factors is variable in sockeye salmon populations. These factors were described in last year's report (Ridgway and Utter, 1964). Sufficient antisera are on hand for extensive testing. The data for the 1964 sockeye salmon samples are given in Table 19.

Both reagents detected significant differences in frequencies between areas. It appears that much of the " H " factor's significance is the result of the high frequencies in three of the four areas south of the Alaska Peninsula, indicating a possible usefulness of this reagent for distinguishing these areas from

Table 17. Reactions of chum salmon erythrocytes from two Puget Sound areas using five rainbow trout isoimmune sera.

Area	Samish			Quilcene			Chi-square results for Samish and Quilcene
Reagent	Total sample	No. positive	Percent positive	Total sample	No. positive	Percent positive	
260	26	12	46	20	0	0	12.5**
269	26	9	35	20	20	100	20.8**
282	26	9	35	20	20	100	20.8**
291	26	9	35	20	4	20	1.15
252	26	14	54	20	14	70	1.18

** Significant at the 1% level.

Table 18. Reactions of Alaskan and British Columbia pink salmon erythrocytes using four rainbow trout isoimmune sera.

Reagent	425			308			504			511		
Area	Total sample	No. positive	Percent positive	Total sample	No. positive	Percent positive	Total sample	No. positive	Percent positive	Total sample	No. positive	Percent positive
Homer	—	—	—	—	—	—	16	10	62	16	9	56
Sheep Bay	25	22	88	25	13	52	25	16	64	25	21	84
Metlakatla	28	21	75	28	16	57	28	7	25	28	12	43
Skeena	24	16	67	24	10	41	24	22	92	24	16	67
Chi-square results		3.3			1.2			24.38**			9.96*	

* Significant at the 5% level.

** Significant at the 1% level.

Table 19. Incidence of the " H " and " C " factors in various North American area samples in 1964.

Area	" H " Factor			" C " Factor		
	Total sample	No. positive	Percent positive	Total sample	No. positive	Percent positive
Kvichak	26	15	58	26	16	62
Branch R.	21	13	62	21	9	42
Naknek	23	12	53	23	19	83
Egegik	21	12	57	21	8	38
Ugashik	25	5	20	25	14	56
Karluk	24	24	100	24	23	96
Kenai	27	15	56	27	18	67
Copper R.	191	170	89	202	102	50
Skeena	30	27	90	30	29	97
Chi-squares results		94.8**			48.0**	

** Significant at the 1% level.

those in Bristol Bay. Interesting frequency differences may also be observed for the " C " factor. Of particular potential value may be the difference between the Skeena and Copper River samples. However, a considerably greater amount of sampling will be required before the usefulness of either factor can be firmly established.

Studies to determine the onset of maturity in salmon by serological means have continued (Ridgway, Klontz and Matsumoto, 1962; Ridgway, 1964; Ridgway and Utter, 1964). As in previous years, maturing female salmon have been found on the high seas as early as February. A collection of samples is currently being made on the high seas to determine if female sockeye salmon show onset of maturity during late summer and early fall. Attempts to develop antisera capable of detecting maturing males have been unsuccessful to date.

Summary

Erythrocytes of sockeye salmon from 11 North American areas were tested using 16 rainbow trout isoimmune reagents. The heterogeneity of reaction frequency between areas detected by most of the reagents is potentially useful for the separation of populations.

Limited blood grouping of pink and chum salmon was carried out with rainbow trout isoimmune sera. Although neither species appeared to cross-react as extensively with these reagents as did sockeye salmon, the reagents may be capable of discriminating populations of both species.

Sockeye salmon serum samples collected during the year were analyzed for the presence of two components, the " H " and " C " factors. Differentiation of major areas or certain runs, on the basis of these components may be possible although more data are needed.

Maturity studies were continued. The limited data obtained substantiated previous findings.

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PACIFIC SALMON MORPHOLOGICAL STUDIES

by Staff

On June 30, 1964, morphological studies relating to the problem of the Protocol were terminated. Pink salmon (Amos, Anas and Pearson, 1963; International North Pacific Fisheries Commission, 1963) and chum salmon (International North Pacific Fisheries Commission, 1964a) were included in these studies although most time and effort was given to sockeye salmon (Fukuhara *et al.*, 1962; and International North Pacific Fisheries Commission, 1961; 1963; 1964a; 1964b). The results reported in these papers dealt almost exclusively with the rationale for, and the application of, discriminant function analysis to the problem of classifying to continent of origin salmon taken on the high seas. Classification analysis was given precedence because of its pertinence to the Protocol problem. This, however, was at the sacrifice of reporting the results of other analyses of our data.

This year's work has been concerned with these analyses of data and the preparation of the following reports:

1. *Multivariate Analysis in Subspecific Classification of Sockeye Salmon,* by F. M. Fukuhara and D. D. Worlund. In our previous sockeye salmon studies, seven morphological characters were utilized in a generalized distance function analysis which provided a means of assessing the morphological variations among virtually all principal populations of North American sockeye salmon and of some Asian sockeye salmon populations. Describing and depicting seven-dimensional relationships between about 100 different samples, however, was formidable.

To achieve a simplified two-dimensional graphical description of morphological variations between all sockeye salmon populations represented in the analysis, we computed two linear functions of the variables which account for about 90% of the inter-area variation. This method shows promise of describing the affinity of samples taken on the high seas to general areas of origin and should be of particular value when applied to sockeye salmon taken in the Gulf of Alaska.

2. *Interspecific Variations in Some Species of* Oncorhynchus, by T. A. Dark and B. J. Landrum. Analyses of morphological variations in some Pacific salmon species are based on data collected from 1955 through 1962 from specimens obtained from salmon-producing streams covering almost the entire ranges of sockeye, pink and chum salmon on the perimeters of the Pacific Ocean and the Bering Sea. This material provides valuable information on intraspecific and interspecific variability of 11 meristic characters which will be useful for racial studies, will define species parameters, and aid in clarification of species relationships. The objectives of the report are: (1) to estimate the population parameters for all available morphological characters for sockeye, pink and chum salmon; (2) to analyze the sources of variation within a species with between-species consideration; and (3) to consider differences between species in developmental responses to similar environment.

3. *Bilateral Asymmetry in Paired Meristic Characters of Pacific Salmon,* by B. J. Landrum. In taxonomic and racial studies, morphological characters usually are obtained from one chosen side of the fish in order to avoid variation caused by asymmetrical development; however, damaged characters result in a statistical and economic loss. Information on the presence and extent of asymmetries in bilaterally paired characters would allow evaluation of the effect of substituting a structure from the opposite side of the fish when the chosen side is unobtainable. Using data from sockeye, pink and chum salmon, the objectives are to determine the presence, extent and direction of asymmetry and to evaluate the effect of substitution of counts from structures on the opposite sides of the fish. The characters considered are: (1) number of lateral line scales, (2) number of gill rakers on the first gill arch, (3) number of branchiostegal rays and (4) number of pectoral fin rays.

4. *The Distribution of Mature Western Alaskan and Kamchatkan Sockeye Salmon* (Oncorhynchus nerka *Walbaum) in the North Pacific Ocean and Bering Sea,* by Betty J. Landrum and Thomas A. Dark. The report summarizes and synthesizes the results of morphological studies on mature sockeye salmon collected in the seven-year period from 1956 through 1962. It reviews the methodology used in application of the discriminant function, examines evidence to support the underlying biological and statistical assumptions, and evaluates the possible effects of not satisfying these assumptions. The spring and summer high seas distributions of mature Asian and North American sockeye salmon are determined from the synthesis of this material.

5. *Vertebral Abnormalities in* Oncorhynchus nerka, O. keta, *and* O. gorbuscha, by Charles D. Gill and Donald M. Fisk. To provide information on the occurrence of abnormal vertebral development in natural populations of salmon, various types of aberrancies, which were considered severe enough to make reliable enumeration of the vertebrae questionable, were described and tabulated from 19,557 radiographs of sockeye, chum and pink salmon vertebral columns.

6. *Collection of Age and Racial Data from Chum Scales,* by J. J. LaLanne and G. Safsten. Methods of enumerating circuli counts and measuring scale lengths are considered and evaluated. Age determination problems involving time of annulus formation, identification of annuli, scale absorption, etc., are considered and solutions suggested.

7. *A Method of Identifying the Continent of Origin of High Seas Chum Salmon,* by J. J. LaLanne. A limited number of 1958-59 high seas samples of mature chum salmon are classified. The analysis employed permits a simplified presentation of area interrelationships and facilitates the use of discriminant function techniques.

8. *Length, Weight and Age of Sockeye, Chum and Pink Salmon from Asia and North America,* by J. J. LaLanne and S. Murai. The report contains tables of length and weight frequencies and mean values grouped by ocean age and sex.

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TABLE 20. Average error in classification weighted according to relative abundance of the contributing stocks of Bristol Bay sockeye salmon in 1963.

Area	Escapement in millions[1]	Relative abundance	Observed percent of misclassification	Weighted value
Branch R.	0.203	0.0571	15.58	0.8896
Egegik R.	0.998	0.2808	5.40	1.5163
Kvichak R.	0.339	0.0954	9.81	0.9359
Naknek R.	0.905	0.2546	4.93	1.2552
Ugashik R.	0.388	0.1092	13.83	1.5102
Wood R.	0.721	0.2029	35.32	7.1664
Total	3.554	1.0000		13.2736

Average errors of misclassification:

for the Bristol Bay population $P_a = 13.2736\%$

for the Kamchatkan population $P_b = 23.0689\%$

(samples 23 through 31, Table 21)

[1] Alaska Department of Fish and Game (1964).

TABLE 21. Classification of high seas samples of mature sockeye salmon in 1963.

Sample number	Sampling date	Sampling position		Sample size	Percent classified		Corrected percent Bristol Bay type*	90% confidence interval*
		Lat.	Long.		Bristol Bay type	Kamchatkan type		
1	5/23	49°39′N	166°03′E	55	38.18	61.82	23.7	6–41
2	5/23	49°46′N	166°38′E	46	32.61	67.39	15.0	0–33
3	5/24	49°30′N	166°19′E	105	33.33	66.67	17.6	0–30
4	5/25	49°29′N	166°35′E	55	21.82	78.18	0	0–15
5	5/29	49°33′N	166°31′E	64	26.56	73.44	5.5	0–20
6	5/29	49°13′N	166°13′E	56	28.57	71.43	8.6	0–24
7	5/29	49°35′N	166°03′E	51	17.65	82.35	0	0–15
8	5/30	49°40′N	166°10′E	44	36.36	63.64	20.9	2–40
9	5/30	49°40′N	166°29′E	47	29.79	70.21	10.6	0–28
10	5/31	49°46′N	166°13′E	139	34.53	65.47	18.0	8–28
11	6/1	49°51′N	165°38′E	45	33.33	66.67	16.1	0–34
12	6/1	49°38′N	165°18′E	47	31.91	68.09	13.9	0–32
13	6/1	49°38′N	165°57′E	53	20.75	79.25	0	0–15
14	6/2	49°05′N	166°55′E	45	31.11	68.89	12.6	0–30
15	6/2	49°05′N	166°17′E	51	21.57	78.43	0	0–15
16	6/2	49°05′N	166°46′E	48	31.25	68.75	12.9	0–30
17	6/3	49°27′N	166°17′E	146	34.93	65.07	18.6	8–29
18	6/4	49°33′N	166°09′E	52	38.46	61.54	24.2	7–42
19	6/4	49°05′N	165°48′E	59	32.20	67.80	14.3	0–30
20	6/5	49°40′N	166°52′E	51	21.57	78.43	0	0–15
21	6/5	49°12′N	165°52′E	39	28.21	71.79	8.1	0–27
22	6/5	49°53′N	166°31′E	47	36.17	63.83	20.6	2–39
23**	6/19	50°26′N	166°36′E	34	20.59	79.41		
24**	6/20	50°53′N	165°57′E	37	18.92	81.08		
25**	6/20	50°26′N	166°18′E	39	30.77	69.23		
26**	6/20	50°53′N	166°27′E	38	28.95	71.05		
27**	6/21	50°55′N	166°35′E	33	27.27	72.73		
28**	6/21	50°55′N	165°28′E	41	9.76	90.24		
29**	6/22	50°15′N	166°06′E	30	33.33	66.67		
30**	6/21	50°55′N	165°09′E	30	26.67	73.33		
31**	6/22	50°56′N	165°28′E	44	11.36	88.64		

* Percentage estimates truncated at 0 and 100.

** Kamchatkan reference samples.

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SOCKEYE SALMON SCALE STUDIES

by James E. Mason

As part of the research for the International North Pacific Fisheries Commission on the problems of the Protocol, scale characters have been analyzed as a method of determining the origin of sockeye salmon caught at sea. Research reported in the annual reports of the Commission as well as by Mosher (1963) and Anas (1964) show that scales may be used for this purpose. This report contains results of classifying sockeye salmon caught in 1963 to continent of origin by discriminant function analysis of scale character data.

Sampling

In Bristol Bay in 1963 samples of sockeye salmon were taken from the Branch, Egegik, Kvichak, Naknek, Ugashik and Wood Rivers approximately at the peak of the respective runs for use as North American standard reference samples. These rivers had a combined escapement of about 3.5 million sockeye (Table 20).

No samples were available from inshore areas of the Kamchatkan mainland or from the Okhotsk Sea for use as Asian standards. The 1963 high seas samples to be classified to continent of origin were collected aboard the Japanese mothership *Meisei Maru* during the period May 23-June 22, 1963. Only those samples consisting of 30 or more maturing sockeye salmon were used.

The criteria for sexual maturity were those used by Dark and Landrum (1964). The 31 samples from the North Pacific Ocean were taken between 49°05′N to 50°56′N and 165°09′E to 166°55′E, and are listed in Table 21.

Interpretation of Scale Characters

Only those scales collected from the "A" zone (page 115, INPFC, 1963), or the preferred scale, were read. The three scale characters chosen for the analysis were defined by Anas (1964) as follows: (1) Circulus count within the first half of the length of the first ocean zone. Abbreviated: 1st ½ (C). (2) The scale length measured across the first three ocean-type circuli (1–3) using the first ocean-type circulus as a starting point, plus the scale length measured across circuli 4–6. Abbreviated: INT. 1+2. (3) The scale length measured across circuli 13–15 using the first ocean-type circulus as a starting point, plus the scale length measured across circuli 16–18. Abbreviated: INT. 5+6.

Anas and Murai (MS 1964) and Anas (1964) made a number of studies of the factors that could cause variation in the basic data within races of sockeye salmon and of the utility of scale characters. These detailed tests have not been repeated for the 1963 scale collections, since the same personnel, equipment, procedures and criteria were used as in previous years. However, the utility of the three characters is shown in Figure 29 by a discriminant function computed from data collected in 1957. These three scale characters distinguished Bristol Bay from Asian sockeye in all years.

Classification Procedures

The discriminant function developed by Anas and Murai (MS 1964) for the 1957 scale-character data was used to compute the percentages of specimens classified as Bristol Bay type sockeye salmon in the 1963 high seas and inshore samples. The observed percentages of misclassified specimens in the 1963 Bristol Bay stream samples were weighted by their respective escapement estimates. The computed average error of misclassification for mature Bristol Bay sockeye salmon was 13.2% in 1963. The corrected percent of

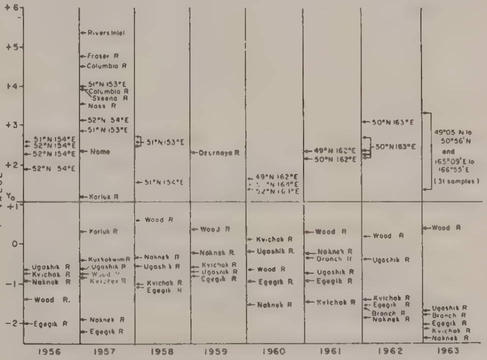

Figure 29. Classification of combined ages of sockeye salmon samples collected from 1956–1963 to either western Alaska or Asia using three scale characters (1st 1/2 (C), INT 1 + 2, and INT 5 + 6) with a discriminant function computed from data collected in 1957.

Bristol Bay type and the 90% confidence intervals are given in Table 21.

In the absence of samples from the Kamchatka Peninsula or the Okhotsk Sea, the nine samples collected after June 5, 1963, aboard the *Meisei Maru* were selected to represent the Kamchatkan population. Considering the stage of maturity, the sampling dates, and the area of sampling, it was assumed that these nine samples were principally of Kamchatkan origin —hence representative of the Kamchatkan population. The computed average error of misclassification for the Kamchatkan population reference sample was 23.1%.

CLASSIFICATION OF NORTH PACIFIC OCEAN SAMPLES

Table 21 shows the corrected percent Bristol Bay sockeye salmon and the 90% confidence intervals for the high seas samples collected May 23 through June 5, 1963, in a relatively small area of the ocean. All point estimates were less than 24.2% Bristol Bay type sockeye salmon.

SUMMARY AND CONCLUSIONS

During May and June of 1963 sockeye salmon were collected in the North Pacific Ocean for scale studies. Samples of 30 or more maturing sockeye salmon were selected. This left 22 samples taken in a relatively small area of the ocean near 49°51′N, 165°–167°E that were suitable for classification to continent of origin. All point estimates of Bristol Bay type sockeye salmon in these samples were less than 24.2%.

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PINK SALMON SCALE STUDIES

by Roger E. Pearson

The primary objective of this study was to use scale characters to classify pink salmon collected on the high seas to regions of origin. Methods of obtaining scale samples and the use of scale characters to classify pink salmon taken on the high seas to continent of origin were discussed by Pearson (1963, 1964a). Subsequent research was directed toward the following objectives: (1) to select a scale axis for use in obtaining the circuli counts and measurements used as scale characters, (2) to test the scale characters for differences between sexes, (3) to examine the effect of fish length on scale characters, and (4) to examine the arithmetic means and standard deviations of scale characters obtained from the 1959 and 1963 collections for differences between regions of origin.

METHOD OF SELECTING A SCALE AXIS

Although circuli counts and measurements can be taken along any axis from the focus, the counts and measurements vary with choice of radial line in the material examined (Pearson, 1964b). To minimize variability between scales, the counts and measurements must be taken from the same radial line (axis) on all scales. Several methods of selecting the same axis were examined, and one method employing the following techniques gave the most consistent results: (1) the longest axis to the annulus was visually selected, (2) seventeen circuli were counted out from the focus along the longest axis to the annulus, (3) one end of a pair of dividers was placed in the center of the focus, (4) the most distant point on the outer periphery of the seventeenth circulus (the greatest distance from the center of the focus) was determined with the dividers and (5) the line formed by the last two points was the scale axis. If the seventeenth circulus could not be used, the sixteenth circulus was used in the same manner.

On some scales (approximately 10–20% of the 1959 samples), the axis was determined, but circuli past the seventeenth were broken or dirty. Rather than discard the scale, a radial line 7.5° to the left of the scale axis or 7.5° to the right of the scale axis was used. In a previous study, the circuli counts and measurements of Table 22 were taken from 20 scales along the scale axis, 7.5° to the left of the scale axis and 7.5° to the right of the scale axis, and examined for differences with one-way analysis of variance tests. The counts and measurements from the three radial lines were not significantly different at the 5% level.

TESTS FOR SEXUAL DIFFERENCES IN SCALE CHARACTERS

Differences in scale characters between the sexes could bias the results of studies for determining the continent of origin of pink salmon caught on the high seas. The 27 characters listed in Table 22 were examined to determine differences due to sex, differences between different spawning areas and to interactions. This was done by use of an approximate two-way analysis of variance design (Snedecor, 1956). If a significant sexual difference was found, the unbiased estimate of the difference was calculated. Since the largest number of pink salmon samples from spawning streams was collected in 1959, that year's samples were used for the tests. All samples from spawning streams with at least 20 males and 20 females were used. The five samples that satisfied these requirements are listed in Table 23. Significant interaction effects were found in characters number 5 and 9 of Table 22. Significant sex effects were found in characters 1, 2, 5 and 9. In respective order, the unbiased estimates of the difference between sexes were 0.398, 0.237, 0.140 and 0.096 circuli greater in males. None of the other 23 characters exhibited significant differences attributable to sex.

Examination of the Effect of Fish Length on Scale Characters

If the scale characters being studied are correlated with fish length, biased results will occur when specimens of non-representative length are collected. Since certain types and sizes of fishing gear will select fish by length, examinations of correlation between fish length and each of the 27 characters of Table 22 were made.

Samples with at least 48 specimens taken from spawning streams in 1959 were used for this test. Six samples satisfied these requirements, the five listed in Table 23 and another from Unalakleet, Alaska. Correlation coefficients were computed for the six spawning stream samples. The average *r* values (the mean *r* of the six samples) and percent variation of the character attributable to the variation in length of fish (Snedecor, 1956) are found in Table 24. The largest percent variation attributable to length in a character was 2.32% in character 13. The results of this examination indicated that length of fish was a negligible source of variation for all 27 characters in Table 22.

Table 22. List of pink salmon scale characters[1].

1. The number of circuli from the focus to the annulus.
2. The number of circuli in the first half of the distance from the focus to the annulus.
3. The number of circuli in the second half of the distance from the focus to the annulus.
4. The number of circuli in the first third of the distance from the focus to the annulus.
5. The number of circuli in the second third of the distance from the focus to the annulus.
6. The number of circuli in the third third of the distance from the focus to the annulus.
7. The number of circuli in the first sixth of the distance from the focus to the annulus.
8. The number of circuli in the second sixth of the distance from the focus to the annulus.
9. The number of circuli in the third sixth of the distance from the focus to the annulus.
10. The number of circuli in the fourth sixth of the distance from the focus to the annulus.
11. The number of circuli in the fifth sixth of the distance from the focus to the annulus.
12. The number of circuli in the sixth sixth of the distance from the focus to the annulus.
13. The width of the narrowest band of three successive circuli interspaces between circuli 1 to 10 (either circuli 1 to 4, 4 to 7, or 7 to 10).
14. The width from the center of the focus to the fifth circulus.[2]
15. The width from the center of the focus to the tenth circulus.[2]
16. The width from the center of the focus to the fifteenth circulus.[2]
17. The width from the canter of the focus to the twentieth circulus.[2]
18. The width from the center of the focus to the twenty-fifth circulus.[2]
19. The width from the center of the focus to the thirtieth circulus.[2]
20. The width from the fifth to the tenth circulus.[2]
21. The width from the tenth to the fifteenth circulus.[2]
22. The width from the fifteenth to the twentieth circulus.[2]
23. The width from the twentieth to the twenty-fifth circulus.[2]
24. The width from the twenty-fifth to the thirtieth circulus.[2]
25. The width from the fifteenth to the thirtieth circulus.[2]
26. The width from the tenth to the twentieth circulus.[2]
27. The width from the twentieth to the thirtieth circulus.[2]

[1] All scales were examined at 100× magnification. Each measurement was to the nearest millimeter.

[2] "Width" replaces "length" as used by Pearson (1964 a).

TABLE 23. Spawning area samples used in tests for sexual differences in meristic characters.

Location	Date	No. of males	No. of females
Petersburg (Sanborn Canal)	8–3–59	28	20
Kodiak Island (Uyak Bay)	8–6–59/	29	31
Alaska Peninsula (Ivanof Bay)	7–30–59	40	25
Alaska Peninsula (Coal Bay)	8–1–59	37	30
Alaska Peninsula (Hook Bay)	8–13–59	27	22

TABLE 24. Average correlation coefficients between fish length and scale character, and percent variation of scale character attributable to the variation in length of fish[1].

Character number[2]	Average r[3]	Percent variation attributable to length[4]
1	0.0620	0.38
2	0.0582	0.34
3	0.0259	0.07
4	0.0572	0.33
5	0.0947	0.90
6	−0.0148	0.02
7	0.0381	0.15
8	0.0527	0.28
9	0.0395	0.16
10	0.0845	0.71
11	0.0033	0.01
12	−0.0266	0.07
13	0.1524	2.32
14	0.0739	0.55
15	0.1149	1.32
16	0.0998	1.00
17	0.1222	1.49
18	0.1403	1.97
19	0.1491	2.22
20	0.1056	1.12
21	0.0074	0.01
22	0.1271	1.62
23	0.1130	1.28
24	0.0890	0.79
25	0.1402	1.97
26	0.0725	0.53
27	0.1259	1.59

[1] Data were obtained from six 1959 samples collected in Alaskan spawning streams.

[2] The character description is found in Table 22.

[3] The average r is an arithmetic mean of six correlation coefficients.

[4] The percent variation attributable to length equals (average $r)^2 \times 100$.

ARITHMETIC MEANS AND STANDARD DEVIATIONS OF SCALE CHARACTERS OBTAINED FROM THE 1959 AND 1963 COLLECTIONS

Arithmetic means and standard deviations of the 27 scale characters were calculated from samples collected in Asia and North America in 1959 (Table 25) and were examined for differences between regions of origin. Many arithmetic mean values differed between eastern Kamchatkan and North American samples. However, Yubetsu River pink salmon had character values similar to Kodiak Island, Unalakleet River and Alaska Peninsula fish. In 1959, scales taken in British Columbia and southeastern Alaska had generally more circuli from the focus to the annulus than scales from Asia, western Alaska and central Alaska. Also, the widths between certain circuli were smaller in British Columbia and southeastern Alaskan scales (characters 17, 19, 20, 21, 24 and 26). In North American samples from British Columbia, southeastern Alaska and central Alaska, the mean values of some characters became progressively larger with an increase in latitude of the spawning region (characters 17 through 27).

In 1963, only North American samples were available. Since scale characters 17 through 27 were best for differentiating fish from North American spawning regions in 1959, scale data were not obtained for characters 1 through 13. The 1963 mean and standard deviation values of characters 14 through 27 (characters 14, 15 and 16 were needed to compute characters 17 through 27) are found in Table 26. As in 1959, the mean values of some characters became progressively larger with an increase in latitude of the spawning region (characters 17 through 21 and 24 through 27). In the British Columbia and southeastern Alaskan samples, the mean values of most scale characters were larger in 1963. The mean values of most scale characters from central Alaskan samples were similar to 1959 values. Correlations between characters have not been examined.

SUMMARY AND CONCLUSIONS

The line formed by the longest radius from the center of the focus to the seventeenth circulus was chosen as the scale axis for 27 circuli counts and measurements. These scale characters were taken along one of the following three radial lines: (1) the previously mentioned scale axis, (2) 7.5° to the left of the scale axis when the first line could not be used, and (3) 7.5° to the right of the scale axis when the first and second lines were not usable.

The scale characters were tested to determine if differences occurred between sexes; four of the 27 characters exhibited significant differences attributable to sex.

Examinations of correlation between fish length and each of the characters were made. The results of these examinations indicated that length of fish

TABLE 25. Arithmetic means and standard deviations of scale characters from the 1959 North American and Asian samples.

Area	Date	Sample size2)	Character number1) 1 Mean	1 s	2 Mean	2 s	3 Mean	3 s	4 Mean	4 s	5 Mean	5 s	6 Mean	6 s	7 Mean	7 s	8 Mean	8 s	9 Mean	9 s
British Columbia																				
Fraser River	9-1	48(45)	26.88	3.33	12.98	1.89	13.90	1.69	8.65	1.45	8.60	1.21	9.63	1.27	4.36	3)	4.29	0.85	4.33	0.75
Rivers Inlet	8-14	61(52)	28.23	2.64	13.39	1.46	14.84	1.62	9.23	1.22	8.43	1.08	10.57	1.25	4.69	3)	4.54	0.67	4.16	0.64
Skeena River	8-14	58(56)	27.72	2.65	13.41	1.64	14.32	1.54	9.31	1.32	8.42	1.05	9.99	1.12	4.82	3)	4.49	0.79	4.09	0.67
Alaska																				
Ketchikan4)	8-16	29(26)	29.59	2.63	14.88	1.49	14.71	1.35	10.60	1.21	8.71	0.96	10.28	1.07	5.51	3)	5.09	0.60	4.28	0.58
Ketchikan4)	8-18	26(24)	29.12	1.86	14.60	1.22	14.52	1.18	10.02	0.96	9.48	0.81	9.62	0.93	5.23	3)	4.79	0.49	4.58	0.73
Petersburg	8-3	48(47)	27.65	1.95	13.77	1.22	13.88	1.17	8.85	1.06	9.16	1.00	9.64	0.86	4.55	3)	4.30	0.80	4.92	0.71
Petersburg4)	8-9	20(20)	27.45	2.35	14.03	1.25	13.43	1.40	9.20	0.94	8.83	0.92	9.43	1.03	4.60	3)	4.60	0.68	4.83	0.65
Kodiak Island	8 6	60(60)	23.35	1.41	11.53	0.89	11.82	0.92	7.98	0.82	6.83	0.66	8.53	0.64	4.07	0.57	3.91	0.42	3.55	0.51
Alaska Peninsula	7-30	65(63)	23.75	1.30	11.60	0.77	12.15	0.84	8.20	0.64	6.82	0.50	8.74	0.67	4.44	0.52	3.76	0.42	3.40	0.34
Alaska Peninsula	8-1	67(66)	22.46	1.32	11.02	0.69	11.43	0.91	7.98	0.58	6.15	0.52	8.33	0.83	4.44	0.46	3.54	0.37	3.04	0.39
Alaska Peninsula	8 13	47(47)	22.84	1.46	11.26	0.86	11.58	0.97	7.98	0.75	6.46	0.66	8.40	0.74	4.48	0.47	3.50	0.52	3.28	0.43
Unalakleet River	7-10, 12	60(60)	23.47	1.31	12.33	0.72	11.14	0.91	8.88	0.75	6.44	0.60	8.15	0.68	4.35	0.63	4.53	0.51	3.45	0.40
Japan																				
Yubetsu River	8-17	52(52)	22.94	2.52	11.88	1.38	11.06	1.36	8.58	1.17	6.51	0.66	7.86	1.08	4.84	0.86	3.74	0.54	3.31	0.37
Siberia																				
East Kamchatka5)	7-4	70(70)	21.11	1.61	10.36	0.84	10.75	1.01	7.14	0.77	6.18	0.64	7.79	0.91	3.70	3)	3.44	0.52	3.22	3)
East Kamchatka6)	7-5	53(53)	20.94	1.41	10.35	0.79	10.59	0.87	7.12	0.63	6.12	0.65	7.70	0.72	3.76	3)	3.36	0.43	3.23	3)

Continued . . .

TABLE 25. Continued.

Area	Date	Sample size[2]	Character number[1]																	
			10		11		12		13		14		15		16		17		18	
			Mean	s	Mean	s	Mean	s	Mean	s	Mean	s	Mean	s	Mean	s	Mean	s	Mean	s
British Columbia																				
Fraser River	9-1	48 (45)	4.27	0.75	4.36	0.71	5.26	0.81	8.54	0.99	23.51	1.83	38.36	3.08	52.98	3.32	67.56	4.36	81.33	5.27
Rivers Inlet	8-14	61 (52)	4.26	0.69	4.67	0.77	5.90	0.78	8.74	1.17	24.89	2.85	40.55	3.63	56.89	4.78	72.79	5.56	87.04	7.07
Skeena River	8-14	58 (56)	4.33	0.73	4.34	0.66	5.66	0.69	8.97	1.20	23.41	2.64	38.87	3.88	56.24	5.24	72.96	5.39	87.69	6.38
Alaska																				
Ketchikan[4]	8-16	29 (26)	4.43	0.65	4.69	0.74	5.59	0.73	8.59	0.98	22.24	1.92	37.52	2.96	55.90	3.99	73.69	4.73	90.41	4.95
Ketchikan[4]	8-18	26 (24)	4.90	0.72	4.25	0.64	5.37	0.58	9.81	1.13	25.04	3.09	42.58	3.07	61.35	4.17	79.12	5.89	98.77	6.31
Petersburg	8-3	48 (47)	4.24	0.61	4.28	0.64	5.35	0.61	10.85	1.49	26.50	2.16	45.80	3.46	62.59	3.94	83.02	5.49	100.63	6.04
Petersburg[4]	8-9	20 (20)	4.00	0.71	4.33	0.65	5.10	0.74	10.30	1.53	25.50	2.41	43.33	4.41	61.00	5.44	82.11	7.20	99.72	8.26
Kodiak Island	8-6	60 (60)	3.28	0.49	3.62	0.46	4.92	0.53	10.55	1.48	27.77	2.78	46.02	4.50	67.55	5.92	86.79	7.27	102.23	7.93
Alaska Peninsula	7-30	65 (63)	3.42	0.41	3.84	0.45	4.90	0.49	11.60	1.46	25.97	2.90	47.73	4.26	70.77	5.90	91.52	7.03	107.76	8.27
Alaska Peninsula	8-1	67 (66)	3.10	0.36	3.64	0.51	4.69	0.56	11.51	1.45	25.42	2.63	48.15	3.78	72.75	5.01	92.69	6.18	109.89	7.25
Alaska Peninsula	8 13	47 (47)	3.18	0.50	3.79	0.52	4.61	0.47	11.18	1.52	25.93	2.89	47.88	4.66	71.86	6.03	91.93	6.09	109.62	7.84
Unalakleet River	7-10, 12	60 (60)	2.99	0.44	3.49	0.33	4.66	0.44	9.12	1.28	27.96	2.74	44.81	3.88	69.19	5.46	90.56	6.83	107.52	7.80
Japan																				
Yubetsu River	8-17	52 (52)	3.20	0.33	3.32	0.58	4.54	0.68	10.71	1.50	26.25	2.61	47.00	3.94	71.82	6.14	94.89	7.97	113.79	9.91
Siberia																				
East Kamchatka[5]	7-4	70 (70)	2.96	[3]	3.23	0.63	4.56	0.49	12.20	1.65	29.50	2.85	50.60	4.09	75.31	6.00	93.58	6.61	111.54	7.98
East Kamchatka[6]	7-5	53 (53)	2.89	[3]	3.26	0.48	4.43	0.45	11.83	1.53	28.95	2.48	50.03	4.26	74.31	5.60	92.42	5.92	110.49	7.04

Continued . . .

TABLE 25. Continued.

Area	Date	Sample size[2]	Character number[1]																	
			19		20		21		22		23		24		25		26		27	
			Mean	s	Mean	s	Mean	s	Mean	s	Mean	s	Mean	s	Mean	s	Mean	s	Mean	s
British Columbia																				
Fraser River	9–1	48 (45)	95.24	6.47	14.84	2.04	14.62	1.86	14.58	1.89	13.78	1.92	13.91	2.39	42.27	3.96	29.30	3.03	27.69	3.07
Rivers Inlet	8–14	61 (52)	100.30	8.03	15.66	2.05	16.34	2.28	15.89	2.60	14.25	2.63	13.27	2.28	43.41	5.36	32.23	3.84	27.52	3.88
Skeena River	8–14	58 (56)	101.80	6.91	15.46	2.10	17.37	2.37	16.72	2.41	14.72	2.21	14.11	2.14	45.56	4.20	34.09	3.55	28.83	3.36
Alaska																				
Ketchikan[4]	8 16	29 (26)	105.14	6.05	15.28	1.56	18.38	2.61	17.79	2.44	16.72	2.42	14.72	2.34	49.24	4.51	36.17	3.61	31.45	3.51
Ketchikan[4]	8–18	26 (24)	114.62	6.84	17.54	1.96	18.77	2.49	17.77	2.30	19.65	2.35	15.85	1.78	53.27	4.03	36.54	3.73	35.50	2.90
Petersburg	8–3	48 (47)	118.17	7.06	19.30	2.61	16.78	2.12	20.43	2.70	17.61	2.54	17.54	2.92	55.59	4.87	37.22	3.87	35.15	3.30
Petersburg[4]	8–9	20 (20)	118.39	8.14	17.83	2.92	17.67	2.28	21.11	2.45	17.61	2.40	18.67	1.71	57.39	3.82	38.78	4.11	36.28	2.61
Kodiak Island	8–6	60 (60)	125.36	9.05	18.25	2.58	21.54	2.73	19.23	2.71	15.45	1.65	23.13	3.61	57.80	5.11	40.77	4.21	38.57	3.89
Alaska Peninsula	7–30	65 (63)	131.47	10.39	21.76	2.09	23.05	2.38	20.74	2.14	16.24	2.28	23.71	4.22	60.69	6.18	43.79	3.71	39.95	5.40
Alaska Peninsula	8–1	67 (66)	136.17	9.64	22.74	1.99	24.60	2.45	19.94	2.33	17.20	2.97	26.28	4.20	63.42	6.81	44.54	4.14	43.48	5.92
Alaska Peninsula	8 13	47 (47)	136.48	10.64	21.95	3.03	23.98	2.52	20.07	1.83	17.69	3.48	26.86	3.97	64.62	6.51	44.05	3.27	44.55	5.94
Unalakleet River	7–10, 12	60 (60)	132.44	8.94	16.85	2.38	24.37	2.42	21.37	2.57	16.96	2.31	24.93	2.97	63.26	5.65	45.74	4.01	41.89	4.48
Japan																				
Yubetsu River	8–17	52 (52)	136.68	12.92	20.75	2.37	24.82	3.04	23.07	3.54	18.89	2.78	22.89	5.01	64.86	8.21	47.89	5.29	41.79	6.11
Siberia																				
East Kamchatka[5]	7–4	70 (70)	138.22	10.24	21.10	2.46	24.71	2.76	18.27	2.17	17.96	3.13	26.68	3.99	62.91	6.34	42.97	3.72	44.64	5.82
East Kamchatka[6]	7–5	53 (53)	136.48	10.54	21.09	2.87	24.27	2.57	18.12	2.13	18.07	2.73	25.98	4.77	62.17	6.47	42.39	3.61	44.05	6.23

[1] The character description is found in Table 22.

[2] The first number indicates the number of scales used to compute the mean and standard deviation. The second number is the sample size found in studies where vertebrae and branchiostegal rays were also examined (Pearson, 1963; 1964b).

[3] The standard deviation was not computed.

[4] Seventy-five mature fish were originally sampled. Most scales were eroded to such an extent that usable data could not be obtained.

[5] The sample was obtained at 58°00′N, 175°00′E.

[6] The sample was obtained at 56°49′N, 173°22′E.

Table 26. Arithmetic means and standard deviations of

Area	Date	Sample size	Character 14		15		16		17
			Mean	*s*	Mean	*s*	Mean	*s*	Mean
Washington									
LaConner	8–22	224	25.17	2.80	41.48	3.85	57.87	4.74	74.21
British Columbia									
Fraser River	9–3, 9	110	26.37	2.80	41.95	3.89	58.86	5.25	75.99
Rivers Inlet	8–6, 7	183	25.27	2.40	41.59	3.63	61.03	4.89	78.68
Bella Coola	8–5	263	23.94	2.59	40.82	3.84	59.71	5.33	76.83
Bella Bella	8–12, 26 ; 9–2	109	25.44	2.88	42.31	4.39	60.74	5.37	77.39
Butedale	7–29 ; 8–4	110	26.39	2.65	43.71	3.63	61.99	5.10	77.82
Skeena River	8–5	240	25.68	2.45	42.60	3.60	61.10	4.81	77.57
Nass River	8–5	180	26.72	2.55	42.80	3.49	62.41	4.89	80.26
Alaska									
Ketchikan	8–8, 9	139	26.53	2.72	42.76	3.76	61.69	5.49	80.26
Wrangell2)	8–11, 12	54	25.50	2.99	42.91	3.31	61.00	4.00	80.93
Baranof Island2)	8–14, 15	56	26.66	2.82	46.32	3.56	65.23	4.89	86.46
Juneau	7–14, 15, 16	62	27.24	2.53	48.23	3.84	67.16	4.79	88.82
Prince William Sound	7–25	203	26.83	2.66	47.69	4.03	67.01	5.31	88.37
Cook Inlet	7–27	199	26.38	2.54	45.84	3.89	67.80	4.59	88.50
Afognak Island	9–	27	25.82	2.32	43.63	4.34	66.70	6.09	86.81
Kodiak Island3)	8–7	163	29.09	2.91	49.56	4.10	71.31	5.24	91.48
Kodiak Island4)	7–22, 23	205	24.66	2.24	45.22	3.88	69.31	5.39	89.96
Alaska Peninsula5)	8–5	207	25.39	2.95	45.21	5.08	70.94	6.22	89.59
Alaska Peninsula6)	8–1, 2	215	27.19	2.61	47.85	3.95	73.51	5.44	92.49

1) The character description is found in Table 22.

2) Three hundred mature fish were originally sampled. Most scales were eroded to such an extent that widths between circuli could not be measured.

3) Zacher Bay.

4) Olga Bay.

5) Ivan Bay.

6) Ivanof Bay.

was a negligible source of variation in the circuli counts and measurements of all 27 characters.

Arithmetic means and standard deviations of the scale characters were calculated from the 1959 and 1963 collections and examined for differences between regions of origin. In the 1959 collection, many scale characters differed between eastern Kamchatkan and North American samples. However, Yubetsu River pink salmon had character values similar to samples from western and central Alaska. Other characters differed between central Alaskan, southeastern Alaskan and British Columbia samples. No 1963 Asian samples were available. Mean values of central Alaskan samples for 1963 were similar to 1959 values, but 1963 mean values of British Columbia and southeastern Alaskan samples were larger than 1959 mean values.

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POPULATION DYNAMICS

by R. A. Fredin

Biometric research on the dynamics of exploited fish populations of the North Pacific Ocean and Pacific Coast of North America is conducted for the purpose scale characters from the 1963 North American samples.

number[1)]

	18		19		20		21		22		23	
s	Mean	*s*	Mean	*s*	Mean	*s*	Mean	*s*	Mean	*s*	Mean	*s*
5.56	90.30	6.62	106.29	7.36	16.31	2.12	16.39	1.99	16.34	2.26	16.09	2.50
6.49	92.01	7.58	108.52	8.41	15.58	1.96	16.91	2.70	17.13	2.41	16.02	2.52
5.82	93.51	7.10	108.55	8.15	16.32	2.05	19.44	2.44	17.65	2.27	14.83	2.65
6.09	91.00	6.99	105.85	7.94	16.88	2.28	18.89	2.54	17.12	2.13	14.17	2.43
5.95	91.35	6.98	106.69	7.91	16.87	2.46	18.43	2.55	16.64	2.28	13.96	2.14
6.26	91.75	7.25	108.14	8.27	17.32	2.38	18.28	2.56	15.83	2.48	13.93	2.31
6.01	92.30	6.69	108.75	7.14	16.92	2.24	18.50	2.40	16.48	2.43	14.73	2.25
6.07	96.33	7.27	111.82	7.47	16.08	2.15	19.61	2.58	17.84	2.61	16.07	2.66
6.69	97.08	7.53	113.28	8.55	16.22	1.99	18.94	2.71	18.57	2.58	16.82	2.47
5.01	99.80	5.51	115.76	6.57	17.41	1.83	18.09	2.08	19.93	2.13	18.87	2.52
5.86	103.53	6.82	122.02	7.43	19.66	2.00	18.91	2.29	21.23	2.45	17.07	2.69
6.81	104.65	7.70	124.21	9.62	20.98	2.27	18.94	2.06	21.66	3.01	15.82	2.11
6.71	104.61	7.47	123.07	9.04	20.86	2.21	19.32	2.19	21.36	2.52	16.24	2.20
5.73	104.25	6.36	126.80	8.54	19.47	2.33	21.96	2.71	20.69	2.67	15.75	2.20
7.78	102.26	8.64	124.85	11.09	17.81	2.57	23.07	3.00	20.11	2.86	15.44	2.22
5.88	106.37	6.99	129.25	9.16	20.48	2.24	21.74	2.44	20.18	2.25	14.88	2.08
6.55	106.26	7.40	130.52	9.37	20.56	2.76	24.09	2.85	20.65	3.13	16.30	2.53
6.73	109.05	8.37	136.31	9.70	19.82	2.83	25.73	2.66	18.66	2.55	19.46	3.60
6.42	110.87	7.49	138.13	9.35	20.67	2.14	25.66	2.69	18.98	2.52	18.38	3.32

Continued . . .

of (1) assessing the current condition and degree of utilization of the stocks, (2) appraising the effects of varying degrees and types of exploitation at different life-history stages on the sustainable yields of individual and mixed stocks and (3) estimating the levels of maximum sustainable yields from the stocks and determining the conditions necessary to achieve them.

The research involves (1) the selection, development or modification of analytical methods or experimental and sampling procedures for estimating population parameters, such as fishing mortality rates, growth rates, natural mortality rates and population size ; (2) construction of mathematical population models for measuring the effects of one or more variables on yield or for determining stock-recruitment relationships ; (3) computer programming and use of computers for carrying out simulation studies ; and (4) compilation and analysis of existing population data.

During the past year, a substantial portion of the work has dealt with specific scientific problems concerning the rationality of high seas salmon fishing, namely, (1) the effect of high seas fishing on yield from a salmon year class, (2) the effect of fishing mixed salmon stocks on management of individual stocks for optimum reproduction and yield and (3) the effect on yield of mortality or other loss associated with the gear used in high seas salmon fishing.

With regard to the effect of high seas fishing on the yield from a salmon year class, scientific problems requiring investigation include determination of the distribution and magnitude of oceanic natural mortality rates of salmon. In this area of research, we have developed methods for estimating natural mortality rates throughout the ocean life of a salmon population for different temporal distributions of mortality. We have undertaken a compilation and analysis of data on the relation between ocean mortality and size of fish. Special methods for estimating oceanic natural mortality rates of salmon during their last and penultimate year of ocean life have been developed.

Table 26. Continued.

			Character number[1]							
			24		25		26		27	
Area	Date	Sample size	Mean	s	Mean	s	Mean	s	Mean	s
Washington										
LaConner	8–22	224	15.99	2.11	48.42	4.32	32.72	3.18	32.08	3.32
British Columbia										
Fraser River	9–3, 9	110	16.51	2.68	49.65	4.87	34.04	4.14	32.53	4.05
Rivers Inlet	8–6, 7	183	15.04	2.46	47.52	4.97	37.09	3.66	29.87	4.06
Bella Coola	8–5	263	14.85	2.79	46.14	4.76	36.01	3.48	29.02	4.04
Bella Bella	8–12, 26 ; 9–2	109	15.34	2.84	45.95	4.42	35.07	3.54	29.30	3.86
Butedale	7–29 ; 8–4	110	16.40	3.54	46.16	5.18	34.11	3.76	30.33	4.50
Skeena River	8–5	240	16.45	3.21	47.65	4.58	34.97	3.90	31.18	3.83
Nass River	8–5	180	15.49	2.81	49.41	4.42	37.46	4.06	31.57	3.13
Alaska										
Ketchikan	8–8, 9	139	16.20	2.80	51.59	4.89	37.50	4.19	33.02	3.82
Wrangell[2]	8–11, 12	54	15.96	3.13	54.76	4.39	38.02	3.37	34.83	3.52
Baranof Island[2]	8–14, 15	56	18.48	3.12	56.79	4.69	40.14	3.37	35.55	3.51
Juneau	7–14, 15, 16	62	19.56	3.83	57.05	6.31	40.60	3.99	35.39	4.61
Prince William Sound	7–25	203	18.46	3.62	56.06	5.30	40.67	3.77	34.70	4.06
Cook Inlet	7–27	199	22.55	3.95	59.00	5.62	42.65	4.04	38.30	4.71
Afognak Island	9–	27	22.59	3.93	58.15	5.93	43.19	4.85	38.04	5.25
Kodiak Island[3]	8–7	163	22.88	4.30	57.94	5.80	41.91	3.53	37.77	5.27
Kodiak Island[4]	7–22, 23	205	24.26	3.54	61.21	5.91	44.74	4.65	40.57	5.02
Alaska Peninsula[5]	8–5	207	27.26	3.14	65.38	5.62	44.39	4.06	46.72	4.87
Alaska Peninsula[6]	8–1, 2	215	27.26	3.40	64.61	5.59	44.64	4.08	45.64	5.00

Concerning the effects of fishing mixed salmon stocks on management of individual stocks for optimum reproduction and yield, we carried out simulated model studies to compare pelagic and coastal yields from mixed salmon stocks when the stocks have different reproductive potentials and where fluctuating environmental conditions prevail.

With regard to the third question concerning the rationality of high seas salmon fishing, we undertook the design of special studies for measuring the loss of fish from gillnets on the high seas.

The research on problems relating to the rationality of high seas salmon fishing will be reported upon in detail as it progresses.

BERING SEA KING CRAB INVESTIGATIONS

by Herbert Shippen

King crab research at the Bureau of Commercial Fisheries Biological Laboratory in Seattle was formally discontinued as of June 30, 1964, and future research by the United States will be conducted by the Biological Laboratory in Auke Bay, Alaska.

Reports on abundance and distribution of crabs in the eastern Bering Sea based upon otter trawl surveys in 1957-1961 are in preparation. A revised yield-per-recruit model which attempts to consider changes in survival and fishing rates apparently resulting from the large increase in intensity of fishing in recent years is also in preparation.

Tag Returns

More than 32,000 male king crabs were released in the eastern Bering Sea by United States investigators from 1955 through 1961. A "spaghetti" type tag was utilized which remains with the crab through successive molts. By the close of 1963, tags from 14% of those released had been returned.

Tags recovered by Japanese fishing operations during 1963 have been received. The *Tokei Maru* fleet returned 449 tags ; the *Dainichi Maru* fleet returned 599. These returns were from the 1956 through 1961 tagging experiments. None of the tags released in 1955 was returned in 1963.

A summary of the number of tagged crabs released by the Bureau of Commercial Fisheries and recovered in the fishery is given in Table 27.

There are 205 tags from the *Tokei Maru* fleet and 310 tags from the *Dainichi Maru* fleet which were recovered in the 1964 fishery and which are not included in this summary table because the data have not yet been

TABLE 27. Summary of United States tagging operations on eastern Bering Sea king crab stocks, 1955–1963.

Year of release	Total no. released	No. returned	Percent returned	Percent returned in two years
1955	1,351	166	12.3	8.8
1956	3,014	515	17.1	8.9
1957	13,782	1,599	11.6	3.4
1958	5,516	914	16.6	5.5
1959	4,442	594	13.4	6.4
1960	1,329	185	13.9	8.9
1961	2,787	612	22.0	22.0

processed.

There has been a noticeable increase in the rate at which tagged crabs have been recovered in recent years which reflects the growing intensity of commercial fishing. Of the 1961 release group, 22% of the tags were returned by the close of 1963 from the Japanese fishery alone. The increase in intensity estimated by this percentage can be considered to be underestimated for no tag recoveries have been received since 1961 from the sizeable Soviet Union fishery.

In addition to Japanese tag returns, United States fishermen returned 10 tags during the past year from the Slime Bank area north of Unimak Island. All 10 tags had been released in the Bering Sea.

MIGRATIONS OF TAGGED KING CRABS

An analysis of the movement of male crabs tagged and released in the eastern Bering Sea by the Bureau of Commercial Fisheries and eventually recovered in the fishery has been prepared by Mr. Robert Simpson and is currently undergoing review.

Movement of crabs between locations of release and recapture appears to be quite random within the general inshore to offshore seasonal " spawning " and " feeding " migrations. For example, more than 11,000 male crabs were tagged and released in 1957 during a three-week period in an area of about 60 square miles. Within one year, 139 of these male crabs were recovered at widely dispersed locations within an area of 4,000 square miles. Some of the crabs had traveled more than 100 miles before recapture. From 1959 through 1963, an additional 900 recoveries were made from the same release group but over an even larger area.

The extreme migration of an individual crab was about 230 miles during a single year of liberty. A crab at liberty for three years was recovered 260 miles from its place of release. About half of the recoveries, however, were made within 50 miles of the release position and 90% within 100 miles.

GROWTH OF IMMATURE KING CRABS

A study of the growth of immature king crabs has been completed by Mr. Douglas Weber, and a manuscript prepared. Field observations reported in this manuscript were begun in 1958 on crabs less than 60 mm in carapace length at Iliuliuk Bay near Unalaska. Crabs longer than 60 mm were found to move offshore, and data on this group were derived from samples collected in the Bering Sea fishery area.

Through analysis of progression of modes in size frequency, Unalaska king crabs were found to attain a size of 60 mm at three years of age. Combination of the Unalaska and Bering Sea fishery data indicates that a male king crab hatched in the eastern Bering Sea attains sexual maturity at 95 mm five years later. A female crab requires 5½ years to attain sexual maturity. The growth of both sexes is similar through the third year of life (80 mm in length). Beyond 80 mm, the amount of growth per molt in the female crab decreases, whereas in the male crab growth per molt remains constant through maturity.

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FIXATION OF DDT IN ESTUARIES

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The history of fish and wildlife losses following applications of pesticides in the past 20 years has stressed the catastrophes that result from acute pollution. Growing evidence suggests, however, that the more subtle changes resulting from sublethal exposures actually may be more disastrous to the continued well-being of some of our wildlife resources.

An extensive literature reports the causal relationship between DDT and lowered viability of embryonic mollusks, fish, and birds. Continued field use of this pesticide has brought about the artificial selection of resistant strains of insects, amphibians, and fish. Usually, detailed laboratory and field studies have been necessary to identify the critical importance of chronic, sublethal levels of pollution as causes of these effects.

We may expect that future studies will identify even less obvious physiological changes in animal populations. Among them might be, for example, changed behavior in response to various environmental factors, such as temperature and salinity. Research on the effects of pesticides on breeding behavior, schooling, catchability, and resistance to stress must assume a high priority if we are to continue to protect and exploit efficiently our commercial fishery stocks.

In an attempt to assess the importance of pesticide pollution in the marine environment, the Bureau of Commercial Fisheries has undertaken a nationwide estuarine monitoring program to identify geographical and seasonal variations in residues of organochlorine pesticides in estuaries with commercially important fisheries. The assumed transient nature of pesticide pollution in drainage basins and the technical difficulties in identifying trace amounts of chemical pollution in large water masses suggested the use of resident bioassay animals in the monitoring program.

Although controlled experiments at our laboratory had demonstrated the extraordinary ability of the eastern oyster (*Crassostrea virginica*) to retrieve and store organochlorine residues, we spent two years evaluating the suitability of other mollusks and fish. We also investigated the importance to the program of sampling frequency and the technology of preparing samples. The study area was the approximately 100 square miles of primary and secondary bays near Pensacola and Gulf Breeze, Florida, where our laboratory is located. These are typical estuarine waters, relatively free from industrial pollution, and important in that they serve as a nursery area for a wide variety of commercial fish and shellfish.

During these studies, we completed several diverse projects which will be reported in detail elsewhere. This paper summarizes certain findings that I consider important to an understanding of estuarine pollution by pesticides.

METHODOLOGY

Advances in the precision of analytical procedures enable us to detect, with confidence, organochlorine residues in biological samples in the range of 7 to 10 ppb. I am unaware of any evidence, however, that tissue residues of this magnitude constitute a health hazard to either vertebrate or invertebrate fauna. The existence of this level of pollution in estuarine waters is quite another matter. We find, under controlled laboratory conditions for example, that this amount of DDT in the water will inhibit 50 percent of the normal amount of shell deposition in oysters, and within 24 hours it will kill 50 to 100 percent of eight species of fish and crustacea that we have tested. We consider it necessary, therefore, to use the most sensitive analytical methods available to interpret the effect of sublethal contamination of the environment. The data reported here result from the use of gas chromatography with electron-capture analytical procedures.

The sensitivity of these procedures makes it imperative that we maintain the integrity of samples. The ubiquity of DDT in some environments makes it difficult to collect uncontaminated samples. Evidence is good, too, of the breakdown and loss of pesticide residues in biological samples that are improperly handled. It is customary to quick-freeze samples and keep them frozen until analysis to prevent such changes. This procedure would impose economically unrealistic requirements in a monitoring program in which we contemplated the collection of about 3000 samples a year to be sent for analysis to us from 10 coastal states from Maine to Washington. Our tests of many of the standard tissue preservatives proved without exception that they failed to preserve intact the organochlorine pesticide residues.

After some searching, we discovered that the addition of anhydrous sodium sulfate to the sample did preserve the tissue without altering the pesticide content. In practice, sodium sulfate in the amount of 3 to 10 times the weight of the sample, depending on its moisture content, is homogenized with the tissue (plankton, oysters, fish) in an electric blender. A dry, free-flowing product results when the sample is alternately chilled and blended. The sample has the appearance of cornmeal; sealed in a screw-top jar, it may be stored at room temperature at least 30 days without deterioration. It may be shipped by surface mail to the analytical laboratory without recourse to freezing or other methods of preservation.

Since this processing is also the first step in the preparation of biological samples for chromatographic analysis, it accomplishes a double objective. We have been using this technique satisfactorily in the Bureau's monitoring program more than a year.

The selection of a sample size adequate to ensure statistical validity poses well-known problems. Obviously, the determination of pesticide residues in large fish and mammals is restricted to analyses of small portions of one or a few tissues in a small number of individuals. Oysters present no such physical problems and their matabolic activity is relatively uninfluenced by age, sex, or size. They remain physiologically active until water temperatures approach freezing, and they pump water through their bodies in excess of 20 hours a day. As a result, we find that analysis of only 12 individuals provides data representative of the population.

When the levels of DDT pollution are low, oysters concentrate it in their tissues at a uniform rate, and flush it from their bodies at a uniform rate when the pollution stops. Consequently, data on pesticide residues derived from oysters sampled periodically are indicative of both the quantity of pollution and the temporal changes.

It is very different with fish; pesticide residues are sequestered primarily in their adipose tissues, and only on starvation are they mobilized and lost. Typically, we find that in a given area young-of-the-year fish have only half as high DDT residues as are found in one-year-olds. Therefore, "monitor" samples must consist of fish of the same age groups to reflect accurately the degree of pollution.

Under laboratory conditions, the uptake of DDT directly from the water by the pinfish, *Lagodon rhomboides*, soon reaches a maximum. Further uptake is balanced by losses through normal metabolic processes. This maximum can be increased significantly, however, by incorporating DDT directly into the diet of the pinfish. Presumably this is why we find that 10 to 20 percent of the pinfish in contaminated wild populations may have DDT residues far in excess of the others in the sample. Correspondingly larger numbers of fish than oysters must be collected to reduce variability between replicate samples.

One of the surprising conclusions to be drawn from our monitoring data in the Pensacola Bay region concerns the concentration of pesticide residues in fauna in restricted areas. DDT residues in pinfish, oysters, and mussels (*Brachidontes recurvus*) regularly reflect the proximity of the collection site to human residential centers. This relation persists despite the fact that DDT is used periodically along many miles of uninhabited reaches of the shoreline. This localization of the residues in fauna geographically near the presumed source of contamination indicates that a large proportion of the DDT is biologically immobilized soon after its entrance into the ecosystem. The precise location of sampling stations may influence greatly our understanding of the area.

DDT RESIDUES IN FIELD SAMPLES

During 1964, we monitored a natural oyster reef at biweekly intervals to determine the level of pollution by organochlorine pesticides. Much of the time, DDT residues fluctuated between 10 and 20 ppb, a level we consider to be of negligible significance. Beginning in October and continuing through December, the concentration abruptly increased to about four times this value. The following year, we also monitored the plankton on which oysters feed in an attempt to determine the source of the DDT. A decisive increase of DDT residues in plankton that occurred in the summer was followed by a similar increase in residues in the oyster population in the fall.

This passage of DDT from the water to plankton to the oyster was a logical sequence of events, but it was only when we had the data on residues at hand and could estimate the time of the initial pollution of the water that we were able to identify the source of the DDT. We found that during July and August field crews carrying on an insect-control program sprayed the windrows of seaweed on the beaches with DDT to kill larvae of the dogfly, *Stomoxys calcitrans*, a noxious, biting pest. The amount of DDT used seemed negligible; in fact, only once in the past two years had we observed a fish kill that appeared to result from this program. At that time, we found small fish and crustaceans dead and dying along a 200-yard stretch of shore and learned later that spray equipment had been washed in the area.

DDT residues in pinfish vary with both the age of the individuals and the source of the sample. Typically, values are below 0.5 ppm although they tend to increase with the age of the fish. Individual fish may have residues in the range of 12 to 14 ppm. Similar residue levels occur in several other species of resident fish routinely sampled in our local monitoring. Consequently, it was not surprising that, when one of our staff fortuitously collected a recently killed common loon, *Gavia immer,* analyses showed DDT residues of 129 ppm in the muscle and 179 ppm in the liver. Other workers have reported similar high concentrations of DDT and its metabolites in fish-eating birds.

We have scattered data that further illustrate the kinetics of DDT in the estuarine habitat. The mullet, *Mugil cephalus,* is a locally common, herbivorous fish that spawns in the late fall. Analyses of ovaries in that period indicate DDT residues in excess of 3 ppm. Recently we made residue analyses of an adult and of a juvenile specimen of the bottle-nose dolphin, *Tursiops truncatus,* which feeds extensively on mullet. Both specimens had residues of about 4 ppm of DDT and its metabolites in heart muscle and approximately 220 ppm in the blubber.

These findings might have been predicted with some confidence in view of the known persistence of DDT, its affinity for fatty tissue, and the relative position of the loon and dolphin in the food web.

DDT RESIDUES IN LABORATORY SAMPLES

What is the significance of these relatively high residues in apparently healthy animals? Laboratory observations on the effects of sublethal exposures to DDT enable us to analyze the entire test population under controlled conditions and so gain a better concept of the full impact of such pollution in the natural habitat.

In the dogfly-control program, slightly more than 130 pounds of pure DDT are used each year. Theoretically this amount, all applied at one time rather than over 2 months and evenly dispersed in the estuary, would give a concentration in excess of 1 ppb in the water. Since the DDT actually is applied along the beaches, heavy precipitation or a high tide could cause a localized concentration of DDT far in excess of this level.

The oyster, exposed to 1 ppb of DDT in flowing seawater in the laboratory, may store 25 ppm or more in its tissues within 10 days. Simultaneously, it may immobilize in its fecal deposits an additional 8 to 10 percent of the entire amount of the DDT flowing through the system. The particulate DDT in these feces then becomes available to such detritus feeders as the polychaete worms which are important links in the invertebrate food chains.

Osyters exposed to 1 ppb of DDT exhibit little obvious damage, but their growth may be reduced by 20 percent or more during the exposure period. This loss would not be observed in the natural habitat however. During the reproductive season, much of the DDT residue is located in the ovary where its effect on productivity is not known.

When DDT-contaminated oyster meats were incorporated in the diet of croakers, *Micropogon undulatus,* at a rate that the total DDT residue approximated 2 ppm, 50 percent of the fiish died within 43 days. When we fed the same diet to brown shrimp, *Penaeus aztecus,* 50 percent died within two weeks. Although losses of this kind are easily documented in the laboratory, they would be almost impossible to detect in nature. Analyses of animals killed by this diet uniformly showed DDT residues lower than those frequently observed in apparently healthy specimens.

Curiously, when we permitted the oyster drill, *Thais haemastoma,* to feed on live oysters having DDT residues of about 50 ppm, the snails suffered no apparent ill-effects and built up DDT residues of less than 4 ppm in their bodies.

CONCLUSIONS

Plankton plays an important role in the introduction of pesticide contamination into the estuarine food web. Filter-feeding animals further concentrate these residues and immobilize significant amounts of DDT in benthic deposits where it becomes available to detritus feeders.

DDT residues may be fatal to predators at different trophic levels depending on the amount ingested at one time. It is probable that higher death rates and significant losses in productivity exist undetected in estuarine fauna contaminated with DDT.

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PESTICIDES IN THE MARINE ENVIRONMENT

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INTRODUCTION

The successful application of DDT to a variety of pest problems during World War II led to a tremendous increase in its use in the following decade. Numerous other synthetic organic pesticides were soon introduced and, almost inevitably, there was an increase in the number of reports of fish and wildlife mortalities following pesticide applications. Since, in general, appropriate dosage rates had been defined, most mortalities were clearly the result of careless accidents and failure to use established precautions in handling.

It is equally clear, in retrospect, that acute toxic effects and possible human health hazards claimed priority in the investigation of pesticide dangers. The effects of long-continued exposure to sublethal concentrations and the kinetics of pesticides in the environment were neglected, and are still poorly understood.

Cottam & Higgins (1946) summarized data showing some of the acute toxic effects on fish, amphibia, crustacea and birds after use of DDT for insect control. The authors concluded their report with a series of recommendations for the use of DDT that is equally valid today. Loosanoff (1947) reported that the spraying of oyster-shell piles for fly control might enhance their value as clutch for oyster spat, because the spray inhibited fouling of the shells by other sedentary animals such as barnacles. It was thus recognized that low concentrations of a pesticide could have useful applications in the marine environment, but it was not known how large a concentration could be used without causing undesirable side effects. Now, two decades later, our data are still inadequate to answer this question fully.

Serious wildlife losses in the southern United States following Fire Ant (*Solenopsis saevissima*) control programmes in 1957–58 alerted the general public to the possible unexpected side effects of pesticide applications. Even earlier, some marine biologists had been concerned that persistent chemical pesticides might be disseminated through drainage basins and accumulate in estuaries. These coastal embayments are the permanent or temporary habitat of a majority of our commercial fish species. Various kinds of crustacea that make up the most valuable marine harvest are, of course, representatives of the same group of animals that insecticides are designed to kill. Particular concern was felt for sedentary animals that are unable to move away from pollution; the oyster might be particularly susceptible because of its tendency to concentrate and store trace chemicals from the surrounding environment.

LABORATORY STUDIES

As a result of this concern, projects were initiated to find out how to evaluate objectively the toxic effects of pesticides on an array of marine animals under controlled laboratory conditions. Earlier physiological work with the Eastern Oyster (*Crassostrea virginica*) had shown the sensitivity of its pumping response to environmental changes (Butler, Wilson & Rick 1960). Fluctuations in temperature and salinity cause detectable changes in water-pumping rates and the character of the shell movements as recorded by a kymograph. Oysters usually remain closed when exposed to organochlorine insecticides at levels above 1 ppm. At lesser concentrations their physiological irritation is shown by spasmodic—almost tetanic—shell movements. If the concentration of the pollutant is decreased just enough so that shell movements appear normal, careful observation demonstrates that the rate of deposition of new shell is significantly below that of oysters of similar age in unpolluted waters. We have found that the rate of shell deposition (growth) in the oyster is a convenient and objective criterion for evaluating its response to sublethal changes in the environment. Statistically significant data may be obtained in 3 or 4 days with samples of as few as ten juvenile oysters (Butler 1961).

The essential condition for measurements of growth in the laboratory is that the oysters be contained in aquaria with a continuously renewed supply of sea water with its natural plankton content. Relatively small aquaria are used, 75 × 27 × 10 cm deep. Our data indicate that the flow of 175 litres of sea water per hour makes them comparable to aquaria of infinite size. Young oysters 40–50 mm long are selected for tests, since juveniles grow throughout the year when held under these conditions. Older oysters frequently cease depositing shell when water temperatures reach our summer maxima of 28–32° C.

In preparation for an experiment, the posterior end of the oyster's valves are ground uniformly smooth to eliminate any new shell growth, without penetrating the shell cavity. This treatment effectively restricts the space available for the soft body tissues but does not damage them, and stimulates the oyster to deposit new shell. This new growth, for 4 days at least, is largely along the longitudinal axis and may amount to as much as 6 or 7 mm.

The Gulf Breeze Laboratory has now completed the testing of nearly 150 of the most widely used pesticides (usually only the technical grade) to determine their relative toxicity to oysters and other estuarine biota. The evaluations permit some measure of judgement in the selection of pesticides for use in areas adjacent to estuaries.

The growth response of oysters to pesticides is not predictable; each compound must be tested, but certain generalizations may now be made. Organochlorine compounds are usually the most toxic; they frequently are deleterious at even the lowest concentrations tested, i.e. 0·0001 ppm; they are more harmful at summer than at winter water temperatures. A few pesticides of widely different chemical nature have a rather critical threshold of toxic effect; oysters exposed for 6 months or more to levels below the threshold exhibit no detectable changes. The organophosphorus compounds are usually somewhat less toxic at summer water temperatures, presumably because they undergo hydrolysis more quickly; a few cause an increase in the rate of shell deposition at concentrations of 0·1 ppm and less—possibly the result of changes in calcium metabolism or, as we have suspected in some cases, due to the incidental control of oyster parasites.

Oysters exposed to 0·001–0·002 ppm of DDT at a temperature of approximately 30° C appear to grow and behave similarly to control groups. However, chemical analyses of their tissues show that DDT is being stored at levels far above that in the environment. Such biological magnification may be as much as 70 000 times, depending on water temperatures, duration of exposure, and concentration of DDT in the surrounding water. DDT, present in an estuary at levels too low to be detected by ordinary chemical methods, could be concentrated in oysters or other animals and thus be incorporated into the food web within a relatively short time.

The suppression of shell growth in the oyster increases uniformly with each ten-fold increase in the concentration of DDT in the range of 0·0001–0·1 ppm at a water temperature of approximately 17° C. Growth is practically nil at the highest concentration, while at the lowest it is approximately 20% that of a control group. Conversely, when such oysters are placed in uncontaminated sea water, DDT residues are flushed from the tissues at regular rates which may be predicted when the initial level is known. Oysters containing a residue of 151 ppm (whole body, wet weight) require approximately 3 months in unpolluted water to lose 95% of the DDT. Significantly, their growth returns to normal after only 10 days of flushing, when the residue is still more than 100 ppm (Fig. 1).

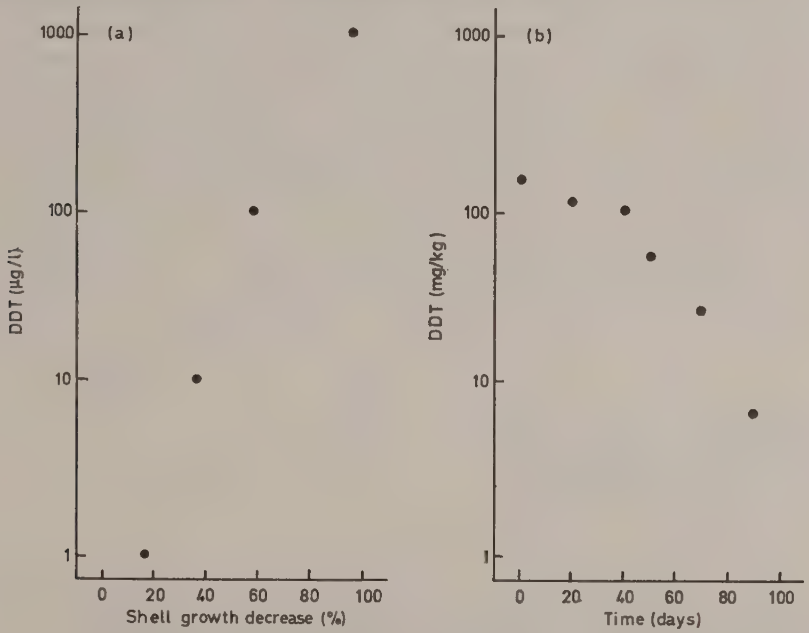

FIG. 1. (a) The relation between the environmental concentration of DDT and the percentage decrease in shell deposition in oysters in 96 h. (b) The relation between an initial body residue in the oyster of 151 ppm and the time required to flush it out in an unpolluted environment. Scales are semilogarithmic.

In the presence of continuous low levels of DDT pollution, oysters build up residues of 25 ppm and more in 1 week without showing harmful effects. When meats of these oysters were fed experimentally to small numbers of shrimp and small fish, the diet killed nearly 50% within 2 days.

Since DDT residues are stored largely in the adipose tissue of vertebrates, there was some question as to the storage site in oysters, which typically contain less than 5% fat. Experiments were conducted in which oysters were exposed to DDT-polluted sea water until they acquired a body burden of approximately 25 ppm. Regional dissection and tissue analysis showed that approximately 67% of the DDT was in the intestinal tract, associated digestive gland, and the gonad. About 26% was in the mantle and gills, and the remainder in the muscle and tissue fluids. In an extension of these experiments, we found that the gonad is a major site of DDT storage and that the gametes themselves may contain 25 ppm or more.

The fact that DDT is stored in the eggs is not surprising in view of their high yolk content, but residues were 35% as high (9 ppm) in the spermatozoa as well. We attempted the laboratory culture of oyster larvae from such highly contaminated gametes. Fertilization and cleavage of the eggs appeared to proceed normally. Unfortunately, both experimental and control cultures were lost at the end of 2 days because of technical difficulties. It is highly questionable, however, whether the larvae could have grown and undergone normal metamorphosis.

The reactions of oysters to different pesticides vary considerably. Many of the chlorinated hydrocarbon compounds inhibit shell deposition significantly at levels ranging from 0·1 to 0·5 ppm. In contrast, herbicides, organophosphorus compounds and the carbamates frequently have little or no effect at concentrations as high as 1 or 2 ppm. In one exceptional instance, when an experimental fungicide containing tin was tested on oysters, shell deposition was completely inhibited at a level of 1 ppm. These oysters were returned to unpolluted water, as is customary, to determine the time required for recovery. Although growth recovery after exposure to even the most toxic pesticides is usually complete in 3 or 4 weeks, these oysters indicated no shell deposition after 8 weeks (although they were still alive). Dissection of the oysters showed that the initial exposure to the chemical had caused an average 35% contraction of the soft tissues. When sacrificed, the oysters had recovered from the exposure and were beginning to deposit new shell, but this was entirely inside the margin of their former body limits.

Table 1. *Accumulation and retention of DDT by molluscs exposed for 7 days to 1·0 μg/l in flowing sea water*

Mollusc	Residue (ppm) After 7 days exposure	After 15 days flushing	After 30 days flushing
Brachidontes recurvus, Hooked Mussel	24	–	–
Crassostrea virginica, Eastern Oyster	26	2·5	1·0
C. gigas, Pacific Oyster	20	16·0	–
Ostrea edulis, European Oyster	15	8·0	4·0
O. equestris, Crested Oyster	23	5·0	–
Mercenaria mercenaria, Northern Quahog	6	0·5	–

It is equally clear that different molluscs react in varying degrees to the same pesticide. In one series of experiments, different species of pelecypods were exposed to DDT under controlled laboratory conditions in aquaria with flowing sea water. After 7 days, sub-samples were analysed for residues and the remaining animals were returned to unpolluted water for 15 days, and some for 30 days, before additional sub-samples were analysed. Rates of uptake and retention were unpredictable and did not appear to be directly related to the water-pumping activity of the particular species (Table 1).

Test conditions must be precisely defined if a reproducible value indicating the toxicity of a compound is to be established. Of special importance is the duration of exposure. The effective concentration of a chemical causing a 50% mortality in a fish population (EC_{50}) may decrease progressively as the exposure period is increased. Telodrin, for example, has a 1-day EC_{50} of 0·003 ppm to a particular fish. The 2-day EC_{50} is 0·0003 ppm and the 11-day EC_{50} is 0·00003 ppm. Some pesticides continue to be toxic at increasingly lower concentrations if the exposure is sufficiently prolonged. Others appear to have a critical threshold of toxicity; continuous exposure below this level has no grossly detectable effect.

FIELD OBSERVATIONS AND MONITORING

The importance of acute toxic pollution may vary greatly depending on the circumstances. In one experiment, DDT was carefully sprayed on a marsh ditch to simulate the effects of commercial mosquito-control operations. Within 1 week there was a 90% mortality in the rather diverse fish population. Within a few months, however, the fish population was as large or larger than before the spraying, and there appeared to be no permanent effects (Croker & Wilson 1965).

It was observed at the time of the fish mortality that various marsh birds were eating the carcasses. No subsequent mortality was reported in the bird populations although the dead fish contained significant amounts of DDT. This is an obvious example of the entrance of DDT into the food web. The possibilities for recycling DDT and other persistent pesticides in the ecosystem can be much more complex.

Random monitoring of plankton, mollusc and fish populations near the Gulf Breeze Laboratory has demonstrated the fluctuating but essentially continuous presence of organochlorine pesticides here. This pollution has resulted in obvious mortalities in some instances. We realize that some significant mortalities of fish and shrimp may be going undetected. Obviously, inhibition of growth in molluscs could result in production losses that are not easily identified. If such losses go long undetected, there may be profound and permanent alterations in the estuarine biota. Of immediate importance is the fact that pesticide residues may build up so that commercial species fail to reproduce, or become unfit for human food.

The extent of pesticide pollution in the estuaries of the North American continent is largely unknown. Casual samples of fish and oysters from different coastal areas indicate that pesticide residues may be rather widely distributed. In some areas, residues were relatively high although there was no ready explanation for their presence. On the basis of these data, it seemed desirable to undertake a nationwide survey of pesticide pollution to determine its seasonal occurrence and centres of concentration. With this knowledge, we may be able to identify its sources and perhaps control the pollution.

In view of the magnitude of the problem from the point of view of distance, manpower, and our own lack of knowledge of critical areas along the coasts, we called upon state and private agencies to assist in evaluating it. To ensure success, it seemed necessary to adopt uniform sampling methods, sample at regular intervals, and have only one agency perform the analyses to assure comparability of data. Finally, the programme needed to be financially adequate to obtain trained personnel and to have sufficient continuity so that the data could be reviewed with some perspective. A programme has been devised which meets these criteria, and methodology has been sufficiently standardized to avoid most technical difficulties.

Research at the Gulf Breeze Laboratory has shown that pesticide residues are present in plankton and a wide variety of fish and molluscs. The oyster, however, is most effective in storing trace amounts occurring in its environment. Further, when pollution clears up, these residues are rather quickly flushed out of the tissues. These attributes and the ubiquity of the oyster in our temperate waters make it most suitable as bioassay animal in a monitoring programme.

The Eastern Oyster (*C. virginica*) is absent in some estuaries where pesticide pollution can be expected to occur. In these areas, other oysters (*C. gigas*, *O. lurida*) and clams (*Mya arenaria*, *Mercenaria mercenaria*) may be substituted as the bioassay species.

We have drawn up contracts or agreements with private agencies and other federal laboratories in twelve states. There are six to twenty-two sites in each of these areas; most of the important shellfish-growing areas on our Atlantic, Gulf and Pacific coasts are included. Samples are collected monthly, processed in the field, and sent to the Gulf Breeze laboratory for analysis by gas chromatography with electron capture methods and confirmation by thin-layer chromatography when necessary.

We anticipate concluding agreements soon with additional agencies so that coastal surveillance for the most widely used chlorinated hydrocarbon pesticides will extend from Maine to Alaska and Hawaii. Such data collected for 1 year will be helpful in pin-pointing trouble areas, but we feel that the programme must continue for several years before we can hope to evaluate this estuarine pollution problem and take effective steps to correct it.

SUMMARY

The increased use of DDT in America after 1946 was identified with accidental mortalities of freshwater fish and wildlife, but it was not until 1958 that the Government appropriated funds to investigate the toxic effects of synthetic organic pesticides on marine biota and to discover the extent to which the agricultural use of pesticides could contaminate the estuarine environment. Laboratory tests have been devised for testing the toxicity of pesticides to marine phytoplankton, crustacea, molluscs and fish, and about 150 chemical compounds have been evaluated.

Environmental pollution by DDT at levels as low as 0·001 ppm causes marked reduction in oyster growth. Molluscs and fish concentrate and store organochlorine pesticides at levels many thousand times greater than that present in their environment Some pesticides cause damage at the lowest levels tested when the exposure is sufficiently long. Others have a critical threshold below which no damage to test animals can be detected.

A nationwide surveillance system has been initiated to monitor permanent mollusc populations and determine the extent of pesticide pollution in North American estuaries. Samples will be analysed monthly for residues of twelve widely used persistent pesticides.

RÉSUMÉ

La corrélation entre l'usage croissant du DDT en Amérique après 1946 et des mortalités accidentelles de poisson de l'eau douce et d'autres animaux a été établie, mais le gouvernement a attendu jusqu'en 1958 pour attribuer des fonds pour examiner les effets toxiques des insecticides organiques synthétiques sur la vie marine, et pour découvrir à quel point l'usage agricole d'insecticides pourrait contaminer le milieu de l'estuaire. On a fait des essais de laboratoire pour vérifier la toxicité de pesticides pour les phytoplanctons marins, les crustacés, les mollusques et les poissons; on a évalué environ 150 composés chimiques.

La pollution du milieu à des niveaux aussi bas que 0,001 ppm cause une réduction marquée de la croissance des huîtres. Les mollusques et les poissons concentrent et amassent les pesticides organochloriques à des niveaux des milliers de fois plus grands que ceux présents dans leur milieu. Certains pesticides causent des dommages aux niveaux examinés les plus bas quand ils sont exposés assez longtemps. D'autres ont une limite critique, au dessous de laquelle aucun dommage aux animaux examinés ne peut être discerné.

Un système national de surveillance a été lancé pour controler les populations permanentes de mollusques et pour dèterminer l'étendue de pollution par les pesticides dans les estuaires de l'Amérique du Nord. Des échantillons seront analysés chaque mois pour les résidus de douze pesticides persistants d'usage général.

ZUSAMMENFASSUNG

Der zunehmende Gebrauch von DDT in Amerika nach 1946 wurde mit zufälligen Todesfallen von Süsswasserfischen und wilden Tieren in Zusammenhang gebracht, aber erst seit 1958 hat die Regierung Geld dazu bestimmt, die toxische Wirkung von synthetischen organischen Pestiziden

auf marine Lebewesen zu erforschen und festzustellen, in welchem Ausmass der Gebrauch von Pestiziden in der Landwirtschaft das Wasser der von den Gezeiten beeinflussten Flüssmündungen verunreinigt. Der Verf. hat Laborversuche entwickelt, um die toxische Wirkung von Pestiziden auf Phytoplankton, Krustazeen, Mollusken und Fische zu prüfen; etwa 150 chemische Präparate sind ausgewertet worden.

Beieiner Verunreinigung der Umgebung mit nur 0,001 ppm DDT nimmt das Austernwachstum merkbar ab. Organochlorine Pestizide werden in Mollusken und Fischen in Mengen angereichert und gelagert, die vieltausendmal grösser sind, als die, die in ihrer Umgebung zu finden sind. Einige Pestizide verursachen Schaden bei niedrigst angewandten Mengen, wenn die Einwirkung lang genug ist. Bei anderen gab es ein kritisches Niveau, unter dem kein Schaden bei den Versuchstieren festgestellt wurde. Man hat ein nationales Überwachungssystem errichtet, um die ständige Molluskenpopulation sowie die Verunreinigung durch Pestizide in nordamerikanischen Gezeitenmündungen zu kontrollieren. Proben sollen monatlich analysiert werden, um Rückstände von 12 vielgebrauchten persistenten Pestiziden festzustellen.

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The Problem of Pesticides in Estuaries

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The Problem of Pesticides in Estuaries

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ABSTRACT

Despite two decades of research, the extent and importance of pesticide pollution in estuaries are poorly understood. Laboratory studies of their acute and chronic toxicity indicate that pesticides may be the cause of ill-defined but significant mortality, loss of production, and, perhaps, changes in the direction of natural selection in estuarine fauna.

Preliminary investigations show the need for a continuing surveillance program to identify the seasonal and geographical distribution of pesticide pollution in estuaries.

The effect of pollution resulting from synthetic organic pesticides has been a problem of grave concern to the management of our wildlife and fishery resources during the past two decades. In 1944, we were only vaguely aware of the extent of the problems, or of what permanent changes might be inflicted on the so-called "balance of nature." Now, 20 years later, our position is not much better. The extensive research of the past has concentrated, and quite properly, on the potential hazard of these chemicals to human health and welfare. Hindsight tells us that there has been too little basic concern about contamination of the environment with persistent chemicals. We knew that pesticides were responsible for some minor wildlife losses; we hoped they were both accidental and incidental. Even in 1963 when mass mortalities involving more than seven million fish were reported to the Public Health Service, less than 10 percent were associated with agricultural operations and an indeterminate amount of this was due to pesticides. There has been an accumulation of a vast amount of data on pesticides but we are still unable to define the problem fully or evaluate the permanent effect of these chemicals on man and his environment.

Our coastal fisheries may be especially vulnerable to the end effects of pesticide applications because of their potential dissemination in drainage systems and final accumulation in estuaries. At the close of World War II there was abundant evidence of the toxicity of DDT to marine fish and shellfish resources, resulting from its application in adjacent salt water marshes for the control of noxious insects. A summary of these data (Cottam and Higgins, 1946) showed clearly the toxicity of DDT to fish, amphibia, crustacea, and birds as well as to the insects it was being used against. Wildlife mortalities varied depending on the method of application and external stresses existing at the time. The authors concluded their report with a series of recommendations for DDT usage which are equally suitable today.

It was also apparent at that time that some pesticides might have beneficial uses in the marine environment. The spraying of oyster cultch with DDT suspensions, for example, enhanced their value in catching the oyster set by inhibiting the fouling of shells with barnacles (Loosanoff, 1947). We could expect then, and we do still, that the use of pesticides would continue and expand. These are essentially labor saving methods and our economy demands that they be developed to the fullest extent consistent with human health and the preservation of our natural resources.

The use of other pesticides steadily increased in the decade following the appearance of DDT as an insect control agent. Relatively few people in this period, even among conservationists, were concerned about the potential hazard to the estuarine environment. It was not until wildlife losses resulting from the fire ant control program in 1957–58 were widely publicized that the general public became aware of the many hazards created by the terrestrial application of organic chemical pesticides.

In 1958, the Department of the Interior first appropriated funds specifically for pesticide research. The immediate aims of our commercial fisheries program were to establish objective toxicity criteria and delineate the extent of the problem in estuaries. These coastal embayments are the permanent or temporary habitat of a majority of our sport

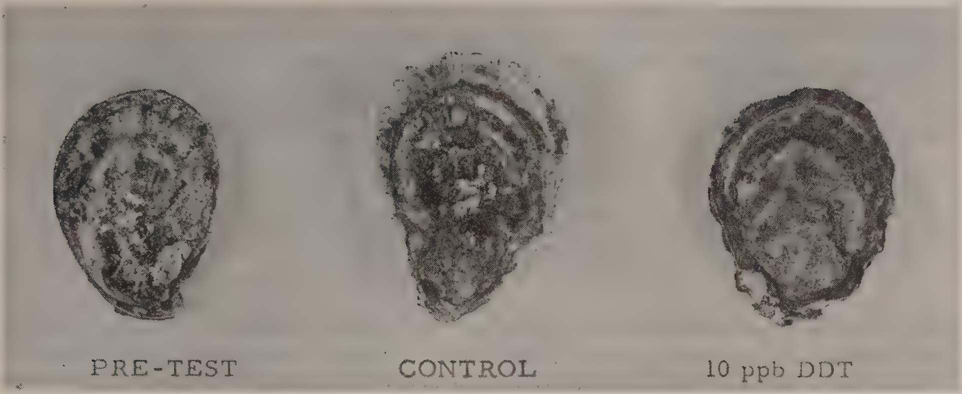

FIGURE 1.—Shell deposition in oysters 1–1½ inches long. All valve edges are ground smooth before test. After 7 days, control oyster has grown approximately ¼ inch. There was a 60% inhibition of growth in the experimental oyster exposed continuously to DDT.

and commercial fishery species. Crabs, lobsters, and shrimp make up our most valuable marine harvest and are marine representatives of the same group that insecticides are designed to kill. In addition, the sedentary mollusks, especially the oyster, are well known for their ability to concentrate in their tissues compounds present in only trace amounts in the estuarine environment.

In view of these facts, projects were undertaken to determine how best to evaluate pesticide toxicity under controlled laboratory conditions. Earlier physiological work with the eastern oyster had shown the sensitivity of its pumping response to changes in the environment (Butler, Wilson and Rick, 1960). Fluctuations in temperature and salinity caused detectable changes in rates of pumping and the character of shell movement as recorded by a kymograph.

Oysters exposed to low levels of polychlorinated hydrocarbon insecticides, or polychlors, quickly showed their physiological irritation by changes in the recorded shell movements. When the concentration of such a pollutant is sufficiently decreased so that shell movements return to a normal pattern, careful observations will demonstrate that the rate of deposition of new shell is significantly below normal. We have found that the rate of shell deposition (growth) in the oyster is a convenient and objective method for evaluating its response to the environment. Statistically valid data may be obtained in 3 or 4 days with samples of as few as 10 oysters (Butler, 1961).

Juvenile oysters measuring about one and a half inches are used in bioassay tests since individuals of this age grow at comparable rates throughout the year when held under similar conditions. The posterior (open) end of the oyster's valves are ground smooth to eliminate soft new membranous shell growth. With care, the shell cavity is not penetrated and this treatment stimulates the oyster to grow immediately and deposit new shell. For four days, at least, this growth is largely unidirectional and may amount to as much as one-quarter of an inch. If such experimental oysters continued to increase in length at the same rate they could attain a length of nearly two feet in a year!

Typical responses of the juvenile oyster to this treatment are shown in Figure 1. The valves of pre-test oysters have been ground uniformly smooth at the beginning of the exposure period. The control oyster has deposited an easily identified rim of new shell in four days. The third oyster represents an experimental animal in which shell deposition or growth has been inhibited by approximately 60 percent by continuous exposure, for example, to 10 parts per billion of DDT.

It has been possible to characterize more than a hundred of the most commonly used pesticides by the criterion of its 96-hour EC_{50},

TABLE 1.—*Variations in shell deposition in oysters exposed to common pesticides*
[Numbers represent average percent decrease or (+) increase in rate of deposition as compared to controls after 96 hours]

Pesticide	Concentration (parts per million)				
	1.0	0.1	0.01	0.001	0.0001
Aldrin	100	86	43	36	11
Endrin	70	40	20	0	
DDT		100	52	0	
DEF	100	50	0		
Baytex	91	+4	0	+14	
Dibrom	76	12	+15	+20	

the effective concentration required to reduce shell deposition by 50 percent in 96 hours. This is a convenient yardstick by which we can visualize the relative toxicity of different chemical pollutants in the estuarine environment.

In typical screening tests, groups of 12 or more oysters in aquaria with flowing sea water are exposed for a period of 4 days to 4 or more dilutions of a pollutant. The pollutant to be tested is mixed in an acetone or tap water stock solution and metered continuously into the test aquaria to maintain a constant level of pollution. The effects of a selected series of typical organic pesticides are summarized in Table 1 to illustrate the variability in oyster reponse. Data are expressed as percent decrease or increase (+) in growth as compared to the control group.

In general, the polychlors such as DDT and endrin are more toxic at summer water temperatures than in the winter, while the reverse is true for many of the organophosphorus compounds such as Baytex. Presumably, this is due to the decreased rate of hydrolysis of the phosphorous compounds in colder water. The enhancement of growth under some conditions as shown in the data has not yet been fully explained. Recent work in our laboratory indicates that, at relatively low concentrations of some pesticides, oyster parasites may be partially controlled without damaging the host oyster. Such conditions may permit a more rapid growth response.

On exposure to very dilute concentrations of DDT, oyster activity and growth appear normal. Chemical analysis of the tissues, however, will show that DDT is being stored as a residue at levels far above that of the environment. Oysters exposed to concentrations of DDT as low as 0.1 part per billion in the surrounding water may concentrate up to 7 parts per million in their tissues in about a month. This biological magnification of 70,000× is indicative of the extent to which trace pollutants in the environment may be concentrated and enter into the food web within a relatively short time.

As the concentration of DDT increased under experimental conditions from levels of 1.0 ppb to 1.0 ppm there is a logarithmic decrease in the rate of oyster growth from about 20 to 90 percent. Conversely, when such affected oysters are placed in uncontaminated circulating sea water, DDT body residues are flushed out of the tissues at regular rates depending on the initial concentration. Oysters having a body burden of 150 ppm of DDT may lose ⅔ of it in 50 days but require another 40 days before residue levels decrease to 6 ppm, a level approximately the accepted standard for raw beef fat. It is significant that growth rates may return to normal after only 10 days in uncontaminated water when body residues are still above 100 ppm.

In the vertebrate body, DDT residues are largely sequestered in the adipose tissues so the question arises as to where DDT residues are stored in oysters which typically contain less than 5% fat. Laboratory experiments were conducted so that experimental oysters were exposed to DDT until they acquired a body burden of approximately 25 ppm. Dissection and tissue analysis showed that approximately 67% of the DDT was in the intestinal tract, associated digestive gland and the gonad. About 26% was found in the muscle and gills, and 7% in the muscle and tissue fluids.

In later work, we found that the gonad stored approximately twice as much as the digestive tract and associated organs. It seemed reasonable to postulate that significant amounts might be stored in the gametes themselves. Here, the residues would be in a critical position to affect directly gamete maturation and viability, cell cleavage, organogenesis, and vitality of the developing larvae. Whether they in fact do, still remains to be demonstrated but the following studies

Table 2.—*Accumulation of DDT and its metabolites in oysters and oyster gametes following 12 days exposure to 1.0 part per billion of DDT*

Sample	Sum of DDT and metabolites (parts per million)
Experimental	
Whole oysters	
10 males	20
10 females	14
12 individuals, unsexed	5–23 Average 10
Gametes	
eggs—5.1 milliliters	25
sperm—0.3 milliliters	9
Control	
Whole oysters	
15 unsexed	0.06
Gametes	
eggs and sperm—1.4 milliliters	Not detectable

clearly indicate the localization of DDT and its metabolites DDE and DDD in the gametes of sexually mature oysters.

Under controlled laboratory conditions, 100 oysters were exposed to 1.0 ppb of DDT for 12 days. The oysters were then dissected, gonads separated from surrounding tissues and minced so that the mature gemetes could be shaken free from other tissues. The gametes from ten or more oysters of each sex were pooled, washed, and centrifuged. Appropriate residue analyses were made using thin-layer chromatographic techniques. Table 2 summarizes the data showing the concentration of DDT and its metabolites in experimental and control samples.

The fact that DDT is stored in the eggs is not surprising in view of their yolk content. The high residue in the spermatozoa needs to be explored further. The logical sequel to this work was the culturing of larvae resulting from these contaminated gametes; this we attempted. Fertilization and cleavage of the eggs appeared to proceed normally but, unfortunately, both experimental and control cultures were lost after 48 hours. The probability of larval cultures containing a body burden of 20–30 ppm of DDT developing into normal oyster populations is not assured since earlier work has shown 100 percent mortality occurs in oyster larval cultures within 6 days on exposure to only 1.0 ppm of DDT (Davis, 1961). If there were survivors, there is the distinct possibility that they might possess unique characteristics, perhaps improving the strain of oysters, perhaps not.

Table 3.—*Relative toxicity of common types of pesticides to estuarine fauna compared to herbicides rated as unity*

Pesticide type	Plankton	Shrimp	Crab	Oyster	Fish
Herbicide	1	1	1	1	1
Insecticide					
Organophosphorus compounds	½	1,000	800	1	2
Polychlorinated hydrocarbon compounds	3	300	100	100	500

Observations of the toxic effects of pesticides under laboratory conditions show that low levels of pollution, causing 10 percent or less mortality, would usually go undetected in the field. Such losses would probably be unimportant in the population dynamics of an abundant species. It is of real concern, however, that such kills are obviously selective. They result from the genetic makeup or physical stresses playing on the individual at the time of exposure. We may be certain that such selective kills are speeding up the processes of natural selection and may be affecting the direction of evolutionary change. The well-established development of DDT-resistant house flies is a good example of this; reportedly 80 other animal species have developed pesticide-resistant strains.

Field research on the nature and extent of pesticide pollution in the marine environment is progressing slowly. The evidence is clear that the persistent chemicals may be transported, both aerially and in ground waters, long distances from the application site. In treated areas, they may lie in the soil or be recycled in the biota for a decade or more. Residues have been reported in presumably unsprayed forest streams, in estuarine plankton, and in a variety of oceanic bottom fish sampled at sea.

Estuarine species respond differentially, but unpredictably, to the different chemical types of pesticides and it is of interest to tabulate such differences quite arbitrarily, recognizing that there will be numerous exceptions. In general, the herbicides as a group are less toxic to marine fauna than other pesticides. In Table 3, herbicides are assigned a toxicity of unity, and the toxicity of other common chemical groups to estuarine fauna are rated relatively. As a group, fish are more sensitive to the polychlorinated hydrocarbons, and the crustacea are most affected by the organophosphorus pesticides.

One difficulty in assessing the importance of pesticide pollution in the estuary arises from the wide variations found in: (a) body residues of apparently healthy individual animals; (b) in the analyses of samples obtained during mass mortalities, and (c) $LC_{50's}$ as determined under experimental conditions. A sample of mixed species of whole fish collected during a mass mortality in South Carolina contained, for example, 0.131 ppm of DDT and its metabolites. Samples of similar fish collected during a kill in Santa Rosa Sound, Florida contained DDT levels of approximately 6 ppm in spot (*Leiostomus xanthurus*) and ghost shrimp (*Callianassa jamaicensis*). In this same area, analyses of our random monitoring samples have shown DDT levels as high as 13.7 ppm in apparently healthy year-old pinfish (*Lagodon rhomboides*). David Hansen (unpublished) of this laboratory has found that even in individual pinfish less than 2 years old from the same area, which presumably have experienced the same environment, DDT residues may vary from less than 1 to 13 ppm in a given sample. Composite samples of reef oysters have been found to contain as high as 1.4 ppm and plankton as much as 0.3 ppm of DDT in samples from the Gulf of Mexico littoral.

It is obvious from our experimental work on oysters that total body residues are of little significance in evaluating the well-being of the animal. Body residues, in general, must be a summation of the individual's experience and are not helpful in the interpretation of any single factor such as length of exposure or exposure concentration. Repetitive data, however, such as periodic monitoring of a population, may be instructive as to the degree and sequence of pollution in a specified area.

When pollutants drain into an estuary, they may be expected to be present for a considerable period of time, although at relatively low levels because of the dilution factor. Some pesticides appear to lose their toxicity when the dilution reaches a certain threshold level. With others, dilution only increases the time factor and, regardless of the low dilution, toxic symptoms eventually appear. Consequently, 24 or 48 hour $LC_{50's}$ have questionable value in determining the impact of pesticide pollution on estuarine biota. The feeling exists that there may be little danger from an insecticide having a 24-hour LC_{50} of 1 ppm since this concentration is not to be expected under field conditions. This same chemical, however, may have a 10-day LC_{50} of 0.03 ppb, a degree of pollution which might well occur.

Jack Lowe (unpublished) of our laboratory has found one pesticide, not in commercial use fortunately, that has a 24-hour LC_{50} of 3.0 ppb to spot. This is lowered to a 48-hour LC_{50} of 0.3 ppb and an 11-day LC_{50} of 0.03 ppb. He also demonstrated that endrin will cause a 100 percent mortality to spot in 5 days at a concentration of 0.1 ppb. Yet this fish can flourish for at least 8 months when continuously exposed to 0.05 ppb of endrin. Many of the animals tested in our laboratory show an extremely sharp threshold of response at very high dilutions of some pesticides.

The estuarine environment is contaminated, then, but to an unknown extent. Is this pollution with pesticides going to increase? From the point of view of volume, probably not very much. There will be new formulations and new areas of application, but domestic use of these chemicals appears to be leveling off. More specific chemicals are being developed and the increased use of baits and biological attractants will prove to be more efficient and far more economical in future pest control operations.

The importance of pesticide pollution from the human health point of view is being investigated on many sides. Biologists and conservationists have the special problem of discovering where wildlife values and estuarine resources are threatened. Today, we are in urgent need of data on the specific areas of pesticide pollution in estuaries, whether the environmental burden is decreasing or increasing, and what the sources of contamination are. Our Bureau's primary interest lies in commercial fisheries products, but there can be no less concern about all other species that enter into the marine food web. The establishment of a continuing monitor system is a must, despite technical difficulties; the use of bioassay animals such as the oyster appears to offer a reasonable approach to this problem.

Technical knowledge is available for remedial action where pollution exists; State, federal and private agencies must take vigorous action to identify and stop pesticide contamination at its source and develop economical methods for cleaning up presently polluted areas.

We must not think that since these chemicals have been identified as pollutants, they can be legislated out of existence. At present, they are too important to our economy. It is our responsibility to support actively the search for safe and effective agents to replace toxic ones now in use.

ACKNOWLEDGMENTS

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THE pH TOLERANCE OF EMBRYOS AND LARVAE OF MERCENARIA MERCENARIA AND CRASSOSTREA VIRGINICA

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The tidal estuarine waters that form the principal habitat of most commercial mollusks are some of the most complex environments in nature. Of the various interacting biological, physical, and chemical factors that affect commercial mollusks in these waters, pH has received less attention than any other major factor. Prytherch (1928) measured the pH at several stations in Milford Harbor and the Milford area of Long Island Sound. He found a pH range during the day from 7.2 to 8.4 and observed that oysters spawned at pH 7.8 to 8.2. Prytherch concluded that low pH inhibited oyster spawning and that oysters in Milford Harbor spawned at high tide because this was the only tidal stage at which the pH was between 7.8 and 8.2. Korringa (1940) quoted Gaarder (1932) and Gaarder and Spärck (1932) who found that larvae of *Ostrea edulis* died when the pH in their oyster polls exceeded 9.0.

In laboratory experiments, Loosanoff and Tommers (1947) found that adult American oysters, *Crassostrea virginica,* kept in pH 4.25 remained open, on an average, 76% of the time, but pumped only 10% as much water as did the controls. Oysters kept at pH 6.75 and 7.00 initially pumped more vigorously than the controls but the rate of pumping later decreased to less than that of the controls.

Although the pH of the open ocean usually ranges from 7.5 to 8.5 (the higher values are at the surface during active photosynthesis), the pH in tidepools, bays, and estuaries may decrease to 7.0 or lower due to dilution and production of H_2S (Sverdrup, Johnson and Fleming, 1942). These inshore areas constitute a major portion of the habitat of commercial bivalves, and Davis and Calabrese (1964) suggested that these regions may be exceedingly important also as the nursery grounds for the larval stages. Since clam and oyster larvae must, at times, encounter a wide range of pH in their natural habitat, it is possible that success or failure of recruitment in some areas may be determined by variations in pH. The present studies were designed to determine the pH tolerance of the embryonic and larval stages of hard clams (*Mercenaria mercenaria*) and American oysters (*Crassostrea virginica*) under laboratory conditions.

Methods

The methods at this laboratory for maintaining spawners and obtaining fertilized eggs throughout the year have been described previously (Loosanoff and Davis, 1963). The effect of pH on the percentage of eggs of clams or oysters that develop into normal straight-hinge larvae was determined by placing a known number of fertilized eggs (usually 10,000 to 15,000) into each of a series of 1-liter polypropylene beakers of filtered, ultraviolet-treated sea water (salinity 27 ± 0.5‰).

The pH of duplicate cultures was adjusted with HCl or NaOH to each of the following levels: 6.00, 6.25, 6.50, 6.75, 7.00, 7.50, 8.00, 8.25, 8.50, 8.75, 9.00, 9.25, and 9.50. Finally, one pair of cultures retained at the pH of our laboratory sea water (7.40–7.70) served as controls. All cultures were kept in a constant-temperature bath at 25° ± 1° C. After 48 hours at the experimental conditions, the larvae from each culture were collected on a stainless steel screen. The larvae were resuspended in a 250-ml. graduated cylinder and, after thorough mixing, a 4-ml. sample was withdrawn and preserved in 5% neutral formalin. The larvae from each sample were then counted and the number of larvae developing normally at each pH was calculated as a percentage of the number of larvae developing normally in control cultures.

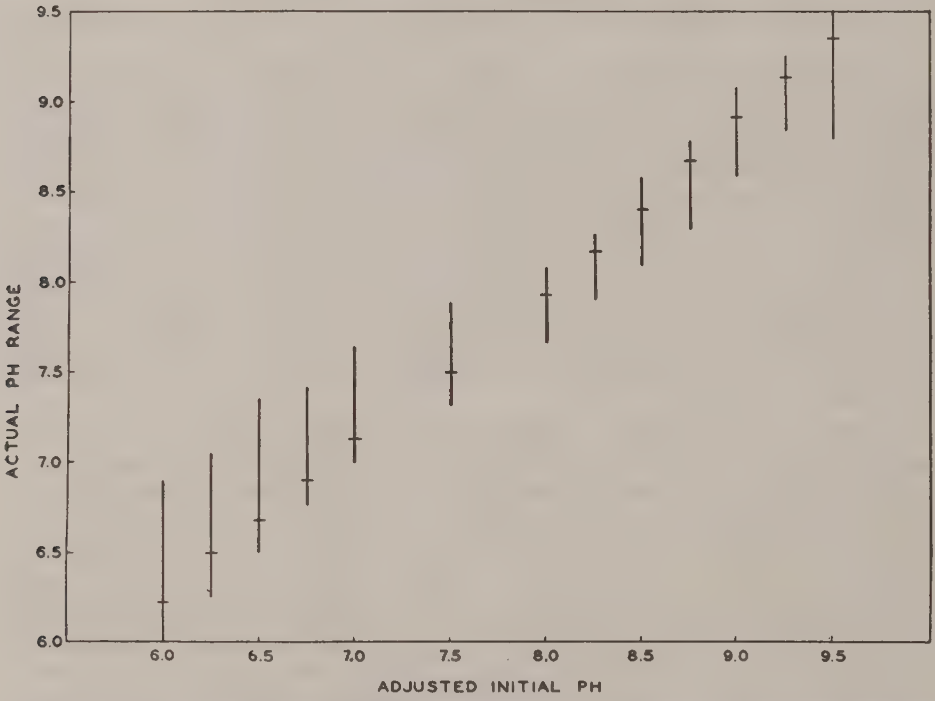

FIGURE 1. Maximum range of pH (vertical line) and average pH (horizontal bar) for each initial pH. The "adjusted initial pH" was established at the beginning of each experiment, and readjusted to this level at 12-hour intervals, by the addition of HCl or NaOH.

To ascertain the effect of pH on survival and growth, a known number of larvae (usually 8000 to 12,000), which had been reared to the 48-hour straight-hinge stage in our normal sea water (pH 7.40–7.70), was placed into each of the series of cultures. The sea water in these beakers was changed every second day and supplemental food, consisting of a mixture of *Isochrysis galbana, Monochrysis lutheri,* and *Chlorella* sp. 580,[1] was added to each beaker daily. The pH of each culture was adjusted to the desired level immediately after each change of sea water by the addition of an appropriate amount of HCl or NaOH. In experiments with clam larvae it was necessary to add a standard dose (50 ppm.) of Sulmet[2] at each change of sea water to prevent disease-induced mortality that was not a direct result of the pH being tested. Since buffers were not used, it was necessary to measure and readjust the pH at approximately 12-hour intervals using a line-operated, solid-state pH meter[3] having a readability of 0.02 pH unit and a repeatability of 0.01 pH unit. The range and average for each initial pH are shown in Figure 1.

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[1] *Chlorella* sp. (Indiana U. Collection #580).

Experiments with clam larvae were terminated after 10 days at the experimental pH levels, when the larvae were 12 days old, because at favorable pH the majority of the larvae had completed larval development and metamorphosis. For similar reasons experiments with oyster larvae were discontinued after 12 days at experimental pH levels, when the larvae were 14 days old.

Quantitative samples were taken from each culture at the termination of an experiment to determine the percentage of larvae surviving and their increase in mean length. In each of these samples, all survivors were counted and 50 clam larvae or 100 oyster larvae from each sample were measured to the nearest 5 μ. The increase in mean length of larvae during the test period was calculated for each pH as a percentage of the increase in mean length of larvae in the control cultures.

The method for determining the number of larvae surviving or the percentage of bivalve eggs developing into normal straight-hinge larvae is accurate to approximately ± 10% (Davis, 1958). Differences of less than 20% in the percentage of eggs developing normally or of larvae surviving a treatment are, therefore, considered insignificant.

Five experiments were with clam larvae and four with oyster larvae. In the first three experiments with clam larvae a standard technique was being developed and various buffer systems were being tested. In these initial experiments citric acid, monobasic potassium phosphate, dibasic sodium phosphate, and Tris (hydroxymethyl aminomethane) were used as buffers in an attempt to stabilize the pH at desired levels. The phosphates and citric acid were not effective in maintaining pH levels below 7.00; these buffers also appeared somewhat toxic to clam larvae. When concentrations of these buffers were high, a white flocculent precipitate was formed in the cultures. Tris was of some help in maintaining relatively stable pH levels above 7.00, but was toxic at pH 8.50 or higher, even though apparently nontoxic at levels below 8.50. A precipitate which adhered to the sides and bottom of the beakers was formed at pH 9.50, with or without Tris. The results of these preliminary experiments are not included in our graphs.

Effect of pH on embryonic development of clams and oysters

The number of clam eggs developing normally within the pH range from 7.00 to 8.75 or of oyster eggs within the range from 6.75 to 8.75 did not vary significantly (Fig. 2). The number of both clam and oyster eggs that developed normally at pH 9.00 was greatly reduced and at 9.25 to 9.50 almost none developed.

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[2] Sulmet (Sodium sulfamethazine)—Trade name of American Cyanamid.

[3] Instrumentation Laboratory's Model 165 LAB-omatic.

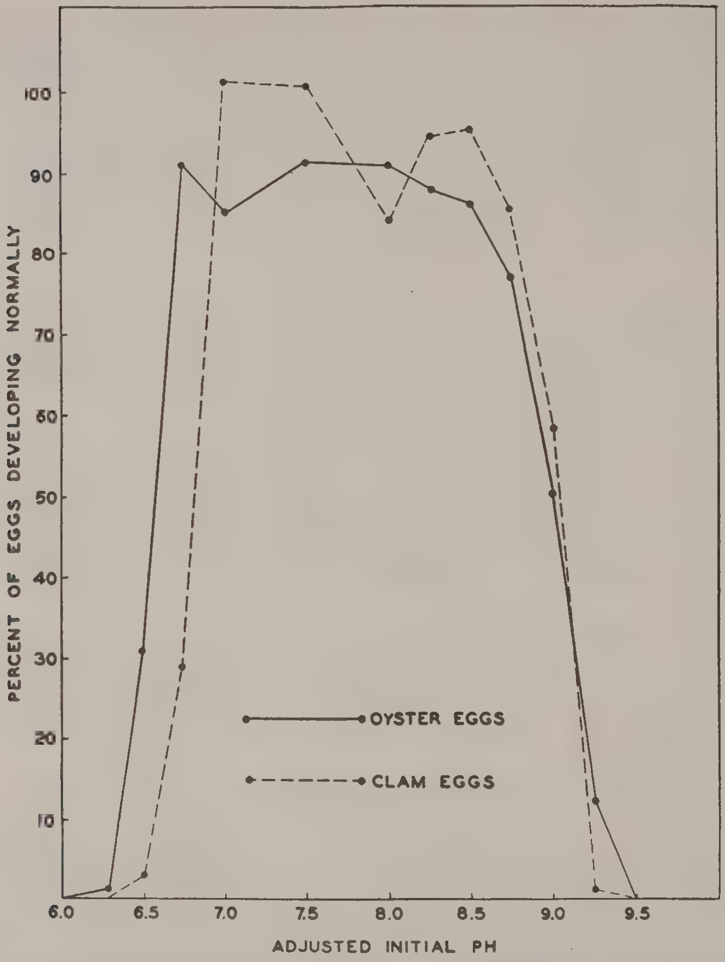

FIGURE 2. Percentage of clam and oyster eggs that developed into normal straight-hinge larvae at different pH levels, expressed as a percentage of the number developing into normal larvae in control cultures.

Clam eggs apparently were not able to tolerate pH values as low as did oyster eggs. At pH 6.75 only 29.5% of the clam eggs developed but 92.4% of the oyster eggs developed normally.

Effect of pH on survival of clam and oyster larvae

Survival of both clam and oyster larvae was approximately normal throughout the pH range from 6.25 to 8.75 (Fig. 3). Oyster larvae were somewhat more tolerant, however, of low pH than clam larvae. At pH 6.00, for example, 21.5% of the oyster larvae survived, but all of the clam larvae died. Survival of both clam and oyster larvae increased sharply from 20% or less at pH 6.00 to approximately 70% at 6.25 and decreased sharply from 70% or better at pH 8.75 to approximately 40% at 9.00. Most of the larvae lived a few days at pH 9.00 although eventually more than 50% died. No larvae of either species survived at 9.25 and higher.

Effect of pH on growth of clam and oyster larvae

The pH range for normal growth was 6.75 to 8.50 for clam larvae and 6.75 to 8.75 for oyster larvae (Fig. 4). The range for normal growth was, therefore, slightly narrower than the range for normal survival. The rate of growth of clam larvae was most rapid at pH 7.50 to 8.00, whereas oyster larvae grew most rapidly at 8.25 to 8.50. Although oyster eggs and larvae survive at lower pH levels than clam eggs and larvae, the optimum pH for growth of oyster larvae was somewhat

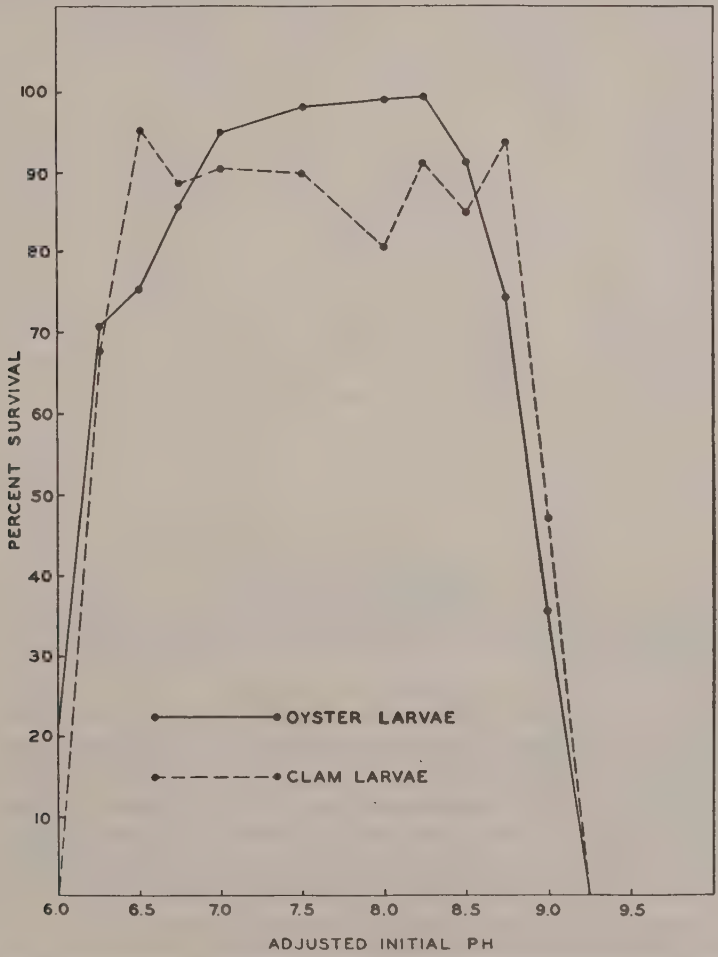

FIGURE 3. Percentage of clam and oyster larvae that survived at different pH levels, expressed as a percentage of survival in control cultures.

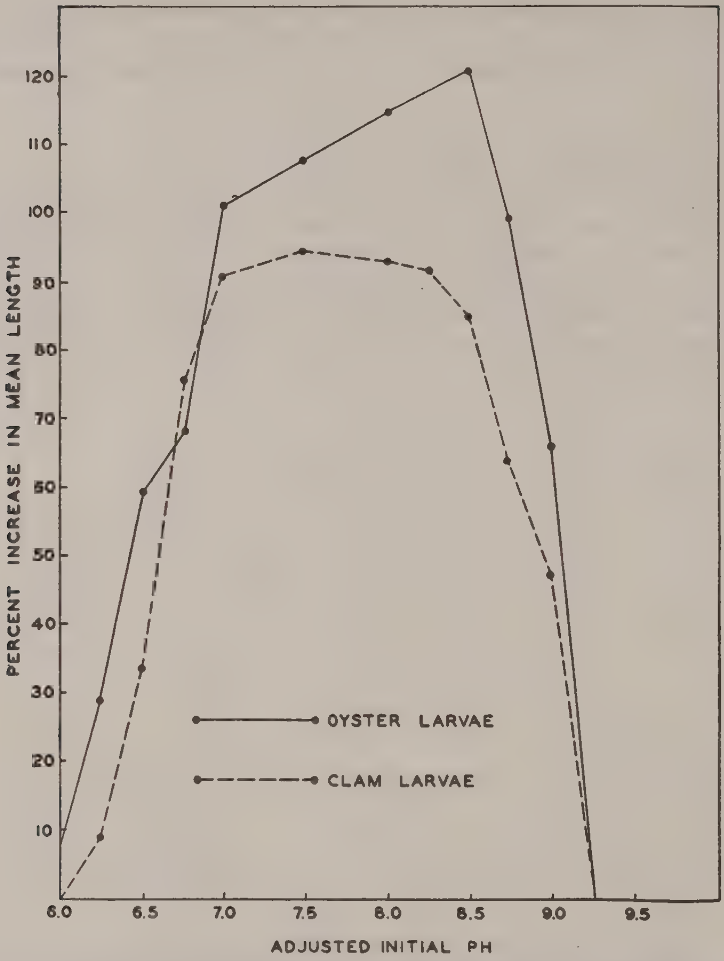

FIGURE 4. Increase in mean length of clam and oyster larvae at different pH levels expressed as a percentage of the increase in mean length of larvae in control cultures. Fifty clam or 100 oyster larvae were measured from each of duplicate cultures at each pH in each of two or more replicate experiments.

higher than the optimum for clam larvae. The rate of growth for both clams and oysters varied only slightly within the pH range 6.75 to 8.50, but below pH 6.75 the rate of growth decreased rapidly. The rate of growth also decreased rapidly at pH values above 8.75 for oysters and above 8.50 for clams. Since the empty shells of dead larvae were not dissolved at the higher pH levels, it was possible to measure them. At pH 9.00 some increase in length had taken place before the larvae died, but at 9.25 to 9.50 there had been no growth.

Implications for distribution and survival in nature

The failure of bivalve larvae to survive and grow at low pH levels did not appear to be an indirect result of the effect of pH on the algal cells added as food. That the food cells were not destroyed by low pH and that they remained in suspension was shown by the fact that they were ingested by the larvae. Since the larvae were fed supplemental food daily, starvation was unlikely even if some algal cells were destroyed. Even those larvae that survived at low pH and had food in their stomachs, however, did not grow appreciably. Gray (1922) found that movement of gill cilia of mussels was more readily inhibited by weak acids which entered the ciliary cells than by strong acids which do not enter the cells readily and, conversely, that weak bases were more efficient restoratives of ciliary movement than strong bases. Because some food was ingested, even at our lowest pH levels, it seems unlikely that failure of these larvae to grow can be attributed to the effect of pH on ciliary movement.

It should be emphasized that clam larvae can survive at pH levels lower than those at which clam eggs can develop normally (Fig. 5). The range for normal

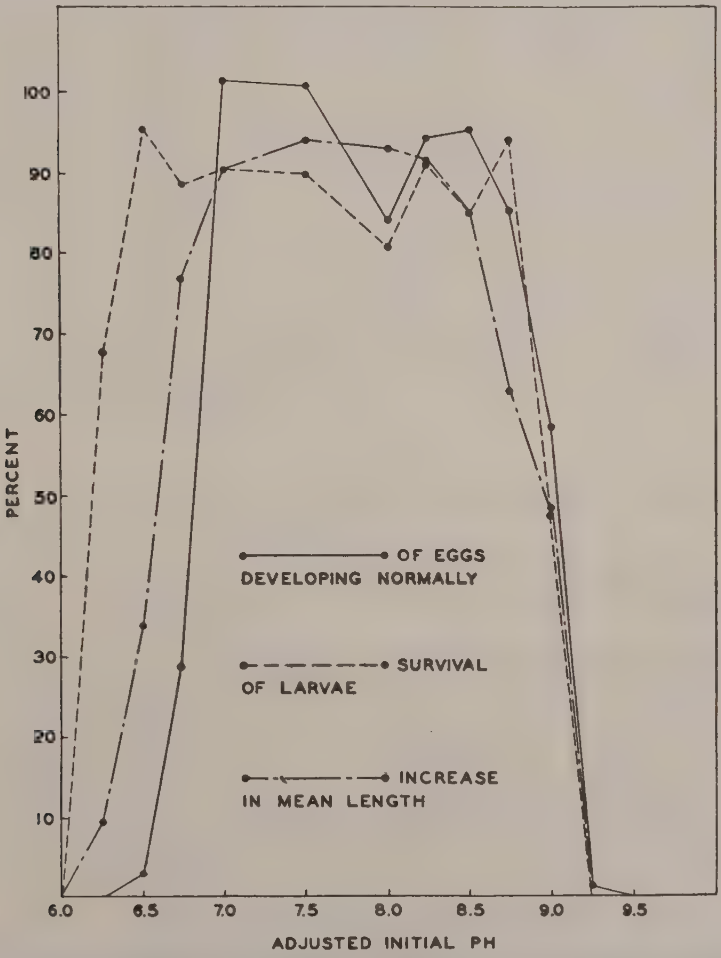

FIGURE 5. The pH tolerance of clam embryos and larvae as indicated by percentage of eggs that developed normally, survival of larvae, and increase in mean length of larvae.

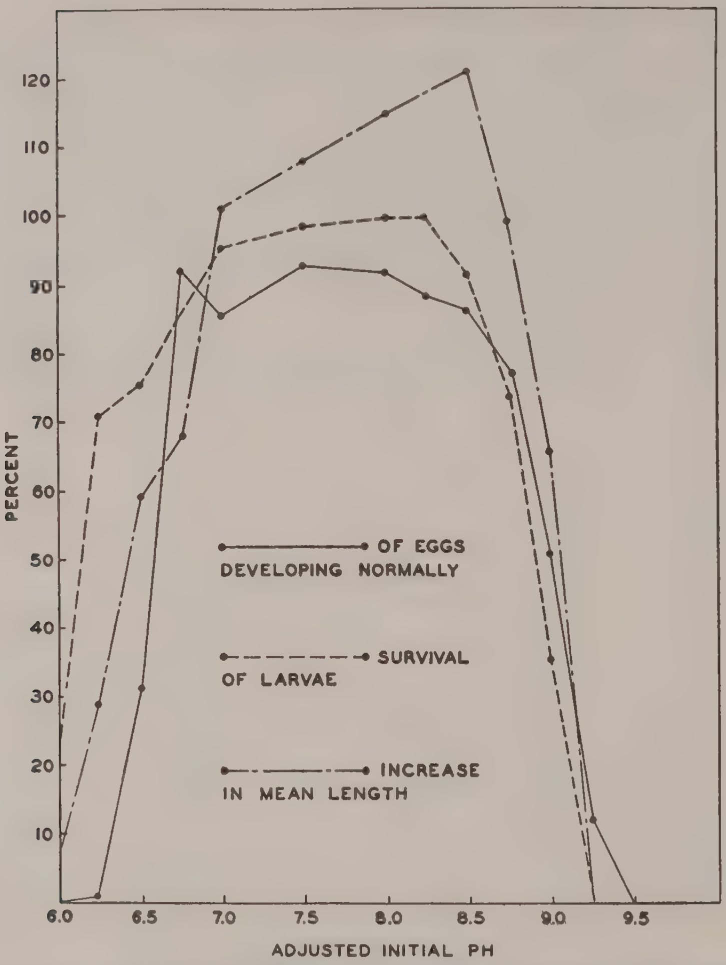

FIG. 6. The pH tolerance of oyster embryos and larvae as indicated by percentage of eggs that developed normally, survival of larvae, and increase in mean length of larvae.

survival of larvae was 6.25 to 8.75, whereas the range for normal embryonic development was only 7.00 to 8.75. In environments with a pH below 7.00, failure of clam eggs to develop normally would be the factor that would limit recruitment of this species. At pH levels 9.00 and above the percentage of clam eggs developing normally, the percentage of larvae surviving, and the percentage increase in mean length all decrease abruptly, so that at high pH levels all three aspects of development limit recruitment of the species. Variations in the percentages of eggs developing normally and of larvae surviving at pH levels between 7.00 and 8.75 were erratic, but all fell within the ± 10% confidence limits of our method. Although the pH ranges for normal survival of clam larvae were 6.25 to 8.75 and those for normal rate of growth were 6.75 to 8.50, the optimum for growth was 7.50 to 8.00. The differences in rates of growth at pH 6.75 to 8.50, however, were slight enough to be negligible in recruitment of this species in nature. The pH of our laboratory sea water (7.40–7.70) was close to optimum for growth of hard clam larvae.

Oyster larvae, like clam larvae, survived at lower pH levels than those at which the eggs developed (Fig. 6). At pH 6.00 none of the oyster eggs developed normally, but 21.5% of the larvae survived. At pH 6.25 the percentage survival of larvae increased sharply, but the increase in the percentage of eggs developing normally was negligible. Most of the oyster eggs developed normally at pH 6.75, whereas a pH of 7.00 was required for most clam eggs to develop. Oysters, therefore, should be able to penetrate into areas of lower pH than clams could tolerate. The range for normal survival of oyster larvae was pH 6.25 to 8.75, and the range for a normal rate of growth of the larvae was 6.75 to 8.75. The optimum pH for growth of oyster larvae, however, was 8.25 to 8.50, *i.e.,* both the optimum and the upper limit for normal growth were somewhat higher than for clam larvae. As with clams, however, the percentage of eggs developing normally, the percentage survival of larvae, and the rate of growth all decrease rapidly at pH 9.00 and above. Since oyster larvae at pH 8.00 to 8.50 outgrew the oyster larvae in the control cultures (pH 7.40–7.70), it was apparent that the pH of our normal laboratory sea water was somewhat too low for the most rapid growth of these larvae.

It can be concluded that for successful recruitment of clams and oysters the pH of the tidal estuarine waters that form their principal habitat must not fall below 7.00 for clams or 6.75 for oysters for any appreciable time. Moreover, neither species could reproduce successfully in waters where the pH remained appreciably above 9.00.

Laboratory experiments have shown that high concentrations of silt can lower the pH of our sea water to 6.40, or below the lower limit for normal development of eggs of hard clams and oysters. It is apparent, therefore, that heavy siltation, or any pollution that can change the pH of tidal estuarine waters, could cause failure of recruitment of hard clams and oysters.

SUMMARY

1. The pH range for normal embryonic development of oysters was 6.75 to 8.75, and for clams, 7.00 to 8.75.

2. More than 68% of the larvae of both clams and oysters survived at pH 6.25 to 8.75. The lower pH limit for survival of oyster larvae was 6.00 and for clam larvae, 6.25.

3. The pH range for normal growth was 6.75 to 8.50 for clam larvae and 6.75 to 8.75 for oyster larvae. The rate of growth of both species dropped rapidly at pH levels below 6.75.

4. The optimum pH for growth was 7.50 to 8.00 for clam larvae and 8.25 to 8.50 for oyster larvae.

5. At pH 9.00 to 9.50 the percentage of eggs that developed normally, the percentage of larvae that survived, and the percentage increase in mean length of both species decreased rapidly.

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Behavior of the Sperm Whale, *Physeter catodon* L.

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INTRODUCTION

Published studies on the behavior of cetaceans in the wild are rare, and we know of no modern ones that attempt to deal with all aspects of the known behavior of any one species. We found that considerable data were recorded by the early whalemen or by their immediate associates. Such information is widely scattered in the older literature, and it seemed desirable to consolidate some of this older information with modern scientific findings.

Despite the fact that the language and the literary style of eighteenth-, nineteenth-, and twentieth-century writers are not always scientific in the modern sense, we were pleased to find that old and new data on the same topic, when both exist, are satisfactorily similar. Therefore we believe that much of the old, or even the popular or semipopular, whaling literature, if treated with care, can be relied upon to provide useful data, especially when there is a correlation in the observations and when the species can be identified without question. For instance, data on the sperm whale, *Physeter catodon* L. (fig. 1), a well-known and wide-ranging species rarely confused by the whalemen with any other cetacean, and seldom confused in the literature, are usually trustworthy.

Because a knowledge of behavior provided a major tool for pursuit of the whale, the whaleman often recorded such data in detail or had it reported in journals by his immediate associates. These early observations, made when whaling techniques forced the whaleman into a more intimate association with his quarry, provide behavioral data that would almost surely be overlooked, or perhaps does not occur, in today's mechanized whaling procedures.

We hope that our work will provide a standard by which to compare the behavior in the wild of other cetaceans so far as it is already known, or as opportunity presents itself for future study. In listing the literature on the sperm

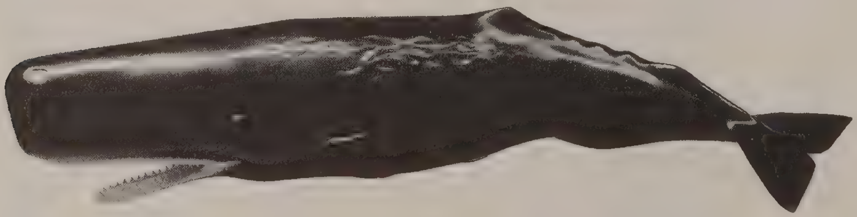

FIG. 1. Model of adult male sperm whale, *Physeter catodon* L., prepared by Dwain Hicks and photographed by Armando Solis of the Los Angeles County Museum, Los Angeles, California.

whale, we have added our own previously unpublished observations (particularly those of Dale Rice, made off the coast of California in recent years).

HABITAT

Location

Townsend (1935), in association with A. C. Watson, charted from American whaling logbook records the catches of 36,908 sperm whales. His charts showed that the distribution of the species was cosmopolitan, except for the summer polar distribution of the males. In the antarctic, an average of 4,145 males were taken each year in the thirteen-year period from 1946–47 to 1958–59 (Crisp, 1962, p. 392). In the Bering Sea, sperm whales are taken up to about 62° N. (Omura, 1955, p. 207; Nasu, 1963, p. 107). The range is thus limited in the Northern Hemisphere, not because the animals are intolerant of colder waters, but because the seas are shallow and the squid are scarce north of this point (Slijper, 1962, p. 343). On the Atlantic side, sperm whales occur north to Davis Strait, Jan Mayen Island, Iceland, North Cape, and the Murmansk coast (Boschma, 1938).

Stranding records (Boschma, 1938) supply further evidence of the cosmopolitan nature of the species. In fact, they are probably a more accurate indication of the wide distribution of the sperm whale, as strandings have been reported where there are no records of local whale catches (Hamilton, 1952, p. 3).

For about 250 years whalemen have been searching for the favorite haunts of the sperm whale, and have learned much about the species' seasonal distribution. Hardship had little effect on the direction of travel taken by the sperm whaler, and consequently whaling records are reliable indicators of the larger concentrations of the animals.

The distribution of whales is determined by two major factors: food and reproductive needs (Townsend, 1935, p. 7). Included in the latter are the needs of the young, as well as the need for a common meeting ground where the adults can copulate. As early as 1840, the keen observer Bennett (II, 183) found that sperm whales are numerous where there are powerful currents or where currents flow in opposite directions, and the food is most abundant. The method of hunting sperm whales with a thermometer—that is, looking for the prey at the boundary line between cold and warm water—has met with some success (Bennett, 1932, p. 71). Clarke (1954*a*, p. 309) also observed that sperm whales are to be found in regions of cold productive waters, as well as in areas where adjacent currents move in opposite directions, as in the equatorial latitudes. This "equatorial divergence" accounts for the grouping of sperm whales on the equator, and in the nineteenth century supported the famous "season on the line" of the American sperm whale fishery of the Pacific (*ibid.*). Even with the primitive whaling methods of the early nineteenth century, as many as eleven sperm whales could be taken in one day in this area (Anonymous, 1828). Between 1910 and 1949, 27.7 per cent of the world catch of sperm whales were taken off the Peruvian and Chilean coasts, where there is an upwelling of the cold productive waters of the Peru Current (Clarke, 1954*a*, p. 309). Nineteen per cent were taken in each of the following areas: (1) the antarctic, (2) West and East Africa, and (3) Japan and Korea; the rest of the world accounted for the remaining 15 per cent (Anonymous, 1950*a*, p. 117).

Although the male sperm whale is almost completely cosmopolitan (Schevill, 1961, p. 205), the females and the young are generally accepted as being limited to the areas between about 40° N. and 40° S. (Slijper, 1962, p. 343). In the eastern North Pacific, females are regularly found as far north as 50° N. In recent years Japanese fleets have taken a few females in the southern Bering Sea (Omura, personal communication to Rice). Salveson (1915, pl. 10) illustrated one female caught off South Georgia (about 55° S.). According to Gilmore (1959, p. 13), the charts show that females are limited by the isotherm of 20°C, but in the eastern North Pacific they are regularly found in waters cooler than 17°C. Schubert (1951, 1955) has concluded that off Chile and Peru there is an orderly segregation from the coast westward, with solitary males occupying waters from 15° to 17°C, bachelor schools in the range from 16° to 18°C, and females at 17°C and warmer. R. Clarke (1962, p. 278), however, could only partly confirm these results. Much remains to be learned about the factors that govern the distribution of the sexes.

Water Depth

The sperm whale is a deepwater species, rarely entering shallow or "green" water (Bennett, 1840, II, 181; Olmstead, 1841, p. 134). If the adjacent water is deep, however, the animals have no fear of approaching the land. They may approach to within 2 to 4 kilometers of oceanic islands (Beale, 1939, p. 8), and Rice observed two of them in deep water less than 2 kilometers off Guadalupe Island. Off Cape San Lucas, Baja California, whaling ships routinely cruised from 20 to 100 kilometers offshore (Clark, 1887, p. 12). On two occasions, sperm whales were killed off Cape Horn within sight of land (*ibid.*, p. 10). The capture of a lone bull was recorded from so close inshore that taking him was dangerous, and every detail of a nearby rock was visible during the capture (Bullen, 1899, p. 340). It has even been postulated that sperm whales are attracted to oceanic islands (Clarke, 1956*a*, p. 443), possibly because there may be local upwelling which increases productivity, thus enlarging the squid population. The species also comes close inshore off Chile and the Galápagos Islands (R. Clarke, 1962, p. 274), and, in Peru and the Azores, catches are made from 6 to 60 kilometers offshore (Clarke, 1953, p. 266).

Clarke (1953, p. 266) believes that sperm whales, either because of their own habit or that of their food, need deep water, and approach a coastline only if it rapidly falls off into deep water. In western Australia, the main catching area is within a 20-kilometer zone outside, and parallel to, the continental shelf (Gates, 1958, p. 564). The shallowest depths of water in which sperm whales have been taken, according to the records, are 73 to 162 meters, off the coasts of America, the Galápagos Islands, and Cape St. Thaddeus (Davis, 1926, p. 398). Scammon (1874, p. 81) recorded captures in depths as shallow as 108 to 126 meters.

Nordhoff (1895, p. 175) noted reports by whalemen that the female sperm whale approached land to give birth to her young, but declared that they had probably drawn an analogy from the known biology of other species of whales, and that the true parturition grounds were not known. According to whalers working off California and British Columbia, females and calves usually are found farther offshore than males.

Migration

Both sexes of the sperm whale migrate. Townsend's (1935) charts, which show an extensive southward movement of all sperm whales as the northern winter season comes on, and a reverse movement at the onset of the winter season south of the equator, give no information about the participation of the sexes in the migrations. Whereas sperm whales are caught the year around in relatively large numbers in the Pacific tropics, catches are more numerous in the southern summer on the coasts of South America and around the Cape of Good Hope. Again, in the Northern Hemisphere on the western grounds (20° to 40° N.), almost all captures occur in the summer months.

Some of the males from the tropics migrate toward the poles each year (Matthews, 1938, p. 154). Graphs of the monthly catches at Natal and Cape Province (*ibid.*, fig. 64) show a peak catch in August, and in South Georgia and the Shetland Islands (*ibid.*, fig. 65) monthly peaks occur in January (South Shetlands) and April (South Georgia). The whalers of Natal believe there is a decided migration of sperm whales from the north in the early southern spring, that is, the northern fall (*ibid.*, p. 156).

A false theory that only the old bulls leave the harems and migrate to the poles appears consistently throughout the older literature, and persists even today (Cockrill, 1958, p. 542), but Matthews (1938, p. 158) has shown that a few young as well as old bulls are found in the antarctic. This migration of adults and a few younger males is also found in the Northern Hemisphere. In the Faeroe Islands, where only males are caught, 109 animals captured ranged from 11 to 19 meters in length. Only nine of these, however, were less than about 15 meters long, so that a fairly uniform stock of older adult males was reported upon (Degerbøl, 1940, pp. 112 f.). Degerbøl (p. 113) also noted that these animals arrived from the south in early summer.

Matthews (1938, p. 159) has presented evidence indicating that the males leave the herd at the height of the pairing season, while still fairly active sexually. They migrate to high southern or northern latitudes, there to rejoin the herds during winter to participate in the general movement toward the equator. It is not known whether or not the males remain in cold waters after their original migration, but it is obvious that there is a yearly recruitment of small males (Jonsgård, 1960, p. 298). A few males do remain in the Azores during the winter, but the main body of males migrates to this region in May (Clarke, 1956*a*, p. 444).

Harem bands also migrate from equatorial waters toward higher latitudes in the summer months, but their range is less extensive than that of the males. Harem bands begin to migrate into the Bonin Islands about the third week of February, with the best catches occurring from July to November (Omura, 1950, p. 107). Nineteenth-century sperm whalers considered the season off Japan to be from April or May to September (Macy, 1877, p. 253). The weather was a factor that induced the whalers to leave in September, rather than remaining longer (Jones, 1861, p. 240). Harem bands arrive in the Azores in May at the same time as the males, and this stock reaches its greatest strength in July (Clarke, 1956*a*, p. 444). The lightest catches in the Azores occur from December to February (Anonymous, 1950*b*, p. 21). These same females and calves are believed to winter in the Cape Verde and Canary Islands (Clarke, 1956*a*, p. 444).

In spite of extensive marking experiments conducted by governmental and other research agencies, little has been learned about sperm whale migrations. Most of the marks have been recovered from whales caught within a few days of the marking, or in the area where they were marked (Brown, 1956, p. 663; 1958, p. 506; Kawakami and Ichihara, 1958, p. 289). During the past few years Japanese and Soviet biologists have obtained a number of significant marking recoveries, still unpublished, showing long-distance movements in the Japan–Kurile Islands–Aleutian Islands area of the western North Pacific (data supplied to the International Whaling Commission by H. Omura and V. A. Arseniev).

The basic fact of sperm whale migration has been known for many decades. Colnett (1798, p. 147) believed the Galápagos Islands to be a breeding and calving ground for sperm whales from the coasts of Mexico and Peru and from the Gulf of Panama. Copulation was frequently observed in the waters near these islands, and young sperm whales "not larger than a young porpoise" were seen there in large numbers (Colnett, 1798). Whalemen continue to believe that the Galápagos Islands waters are a calving ground (R. Clarke, 1962, p. 278). To some extent the Azores are also a calving ground, but it is believed that conception has occurred the previous spring well to the southward, where the main part of the stock spends the winter (Clarke, 1956*c*, p. 271).

Sperm whales were described as "making a passage" when they were seen migrating from one ground to another. Bullen (1899, p. 117) has described their behavior at that time: "The whale was making a passage, turning neither to the right nor left as he went. His risings and number of spouts while up as well as the time he remained below were as regular as the progress of a clock and could be counted upon with as much certainty." Referring to the migration to the Galápagos, Colnett (1798, p. 147) stated: "I have seen the whales, as it were, coming from the main and passing, as it were, from the dawn of day to night, in one extended line, as if they were in haste to reach the Galapagos." Clarke (1954*a*, p. 306) affirms that sperm whales, when migrating, are sometimes encountered in herds of hundreds of animals. When "making a passage" the sperm whales traveled so fast that it was difficult or impossible for the old sailing vessels to catch them (Bennett, 1840, II, 172).

SOCIAL BEHAVIOR

Social Organization

Bennett (1840, II, 171 f.) has described the types of social organization he found in sperm whales: (1) Schools are composed of from twenty to fifty cows and calves, and at least one adult bull. (2) Pods are smaller associations of half-grown males. Pods of fully grown males may occur, but these adults usually roam the oceans singly. (3) Bodies are associations formed by the coalescing of two or more schools. These large assemblages are migrating, and proceed steadfastly in one direction. They move at too high a speed to have been caught by the old whaling methods.

Basically, these groupings as described are valid today. One of us (Rice) can, however, provide a more detailed description of the schools now encountered off the California coast, based on information from modern whalemen from the San Francisco Bay area, personal observation at sea, and examination of the animals brought into the whaling stations near San Francisco. There are three rather distinct associations of sperm whales in the waters off California: (1) Large, often tightly packed, schools of about twelve to fifty animals consist of immature females, pregnant adult females, lactating females with calves, immature males, and puberal males up to 11 meters in length, with testes weighing up to 0.8 kg each (mean testis weight at sexual maturity is about 0.5 kg; in old males testis weight may reach 10 kg). (2) Loose associations are formed by young adult males ranging from 10.5 to 14 meters in length. Up to a dozen whales may be scattered over an area 5 to 10 km square. These animals do not gather into tight schools, but apparently move from area to area more or less as a unit. (3) There are also solitary old males 12 to 17 meters long.

Category 2 grades imperceptibly into category 3. Often a large old male is found close to the schools of females (category 1). The widely held harem concept may be erroneous. There may be no males, or one or more large adult males, with each school of females, and usually several smaller, but sexually mature, males accompany each school of females.

Sperm whales resemble many markedly polygamous mammals in that the male greatly exceeds the female in size, and shows a second spurt of growth at sexual maturity (Nishiwaki *et al.*, 1958, p. 145), as is true of the northern fur seal, ***Callorhinus ursinus***, according to Scheffer and Wilke (1953, p. 134).

Counts of the animals in schools of sperm whales usually are only estimates, for while some members of a school are surfacing, others may be diving (Hopkins, 1922, p. 54; Bennett, 1840, II, 175). The number of animals in harem-type groups varies widely, but recorded estimates or generalizations include the following: three (D. K. Caldwell, personal observation in the Gulf of Mexico at 28° 53′ N., 87° 57′ W., July 26, 1956); twelve to several hundred (Beale, 1839, p. 51; Bennett, 1840, I, 392; Leslie, 1850, p. 71; Scammon, 1874, p. 77; Clark, 1887, p. 212; Van Beneden, 1889, p. 542; Hammond, 1901, pp. 153, 168; Beane, 1905, p. 148; Andrews, 1916, p. 94; Hopkins, 1922, p. 328; Pike, 1956, p. 5; Clarke, 1956*c*, pp. 271, 279; Kawakami and Ichihara, 1958, p. 289; Cabrera and Yepes, 1960, p. 20); and one herd, which appears from the description to have been migrating, was estimated at "well over 1,000" (Boyer, 1946, p. 96).

The number of adult bulls associated with the so-called harem also varies. It has been recorded on specific occasions, or generalized as one to four (Beale, 1839, p. 51; Bennett, 1840, II, 171; Scammon, 1874, p. 77; Macy, 1877, p. 212; Van Beneden, 1889, p. 542; Bullen, 1899, p. 36; Hopkins, 1922, p. 309; Tripp, 1938, p. 236; Haley, 1948, p. 268; Pike, 1956, p. 5; Clarke, 1956*c*, p. 279). Fitzsimmons (1920, p. 215) recorded one to a dozen, but the higher number may be questioned in view of the lower estimates of experienced whalemen.

Adult bulls sometimes withdraw a short distance from the main body of females and calves. Bullen (1899, p. 36) referred to a small pod of cows with one or two bulls lying to windward. Van Beneden (1889, p. 542), noting that the bulls lie 1,000 to 2,000 meters distant and are sometimes found at the head of the band, sometimes at the side, or rarely at the rear, stated that these males exercise a protective function toward the females. Rosenblum (1962) reports that bachelor groups may be found some 4 to 16 kilometers from the females.

The older bulls not associated with a harem usually travel alone (Beale, 1839, p. 51; Bennett, 1840, II, 171; Macy, 1877, p. 63). They may, however, form small groups (Bennett, 1840, II, 171). Bullen (1899, p. 335), in fact, observed a huge school of large-sized bull sperm whales on the Solander grounds, and Hammond (1901, p. 126) recorded a school of a dozen or more. The generally held assumption that the solitary old males join the herds and engage in breeding may be erroneous. Some whalers believe that such males are more or less "outcasts," that they live alone the year around, and that most of the breeding is done by the younger adult males that remain with the pods of females.

Clarke (1956*c*, p. 278) listed two types of aggregations in the Azores which are not described elsewhere. They are (1) schools consisting predominantly of pregnant females, and (2) schools of mixed juvenile males and females, weaned but still quite young. The school of calves noted by Murphy (1947, p. 39), one of which was captured and measured at 7.4 meters, was perhaps of the latter type. The captured animal was a male and many large squid drifted from its gullet at capture.

It has been postulated that there is an increasing tendency toward solitude as the migrating male approaches the antarctic (R. Clarke, 1962, p. 278). Clarke (*ibid.*) found that, whereas only 4 per cent of the bulls sighted on an equatorial cruise were solitary, 56 per cent of those sighted off Chile and Peru (latitudes 28° and 36° S.) were singles. Large pods of males, however, are also found in the antarctic (Ash, 1962, p. 63), as well as the solitary males sighted there by Clarke and Rudd (1954, p. 92) and Lillie (1955, p. 88). Some of the available data suggest that antarctic males tend to aggregate at new and full moons, and to disperse at other times (Holm and Jonsgård, 1959, p. 182).

There also is evidence of the aggregation of mature bulls in the Faeroe Islands. Groups of two, three, four, and fourteen have been recorded (Degerbøl, 1940, p. 109). In addition, a "considerable herd" has been observed in this area (Risting, 1922, p. 209), and "large herds" of animals presumed to be males have also been sighted in Iceland (Iverson, 1955, p. 366).

Young bulls beyond the calf stage, but not fully mature, travel in loose associations, or pods, of various sizes. Although Rice found an upper limit of about a dozen in California waters, Gilmore (1957) recorded a stranding of twenty-two immature bulls at La Paz, Baja California. The stranding of thirty-six bulls and one female at Perkins Island, Tasmania, has also been reported (Lillie, 1915, p. 118), but it is likely that all thirty-seven were bulls (Gilmore, 1959, p. 14).

Parental Behavior

The nursing period lasts thirteen months, according to Clarke (1956*a*, p. 443), whereas Nishiwaki *et al.* (1958, p. 146) estimate twelve months. During the nursing period the mother exercises protective behavior toward the young which frequently overcomes strong fear reactions. This behavior has been detailed in another contribution to this volume by Caldwell and Caldwell; here it is necessary only to note that if the young is wounded, the mother, and frequently other females of the same herd, remain near it until it dies or recovers.

In nursing, the mother lies on her side and the infant suckles at the angle of the mouth because of the underslung jaw (Bennett, 1840, II, 179). Bullen (1899, p. 278) gives a detailed description of nursing by a 4.5-meter calf: "The mother lay on her side, with the breast nearly out of the water's edge; while the calf, lying parallel to the parent with the head in the same direction held the teat sideways in the angle of the jaw with its snout protruding from the surface."

Without evidence, Ash (1962, p. 15) guesses at the existence of an "auntie" in sperm whales, another female of the herd or group which aids the mother in rearing the young. Such behavior, which is found in the bottlenose dolphin, *Tursiops truncatus*, the elephants *Loxodonta africana* and *Elephas maximus*, the African lion, *Panthera leo*, and even to a slight degree in the Cairo spiny mouse, *Acomys cahirinus*, is purely theoretical for the sperm whale. It would seem possible, however, in harem bands.

The male assumes no direct protective function toward his offspring (Bennett, 1840, II, 179). A "harem master," however, may offer incidental protection in his occasional defense of the herd (Van Beneden, 1889, p. 542).

Sexual Behavior

Sexual maturity.—There is general agreement upon the size of females at sexual maturity. Matthews (1938, p. 144) estimated 9.0 to 9.5 meters for the Natal group. Clarke (1956*a*, p. 442) estimated about 9 meters for the Azores group, and, in the North Pacific, Mizue (1950, p. 117) placed the minimum at about 9 meters, although at about 12 meters some animals still were not mature. In the North Pacific most females more than about 12 meters long had bred several times (Nishiwaki and Hibiya, 1951, p. 165).

The age of the female at sexual maturity has recently been estimated at about nine years (Ohsumi *et al.*, 1963, p. 29), which is probably more accurate than Matthews' (1938, p. 144) earlier speculative estimate of fifteen months, and the estimate of four years by Nishiwaki *et al.* (1958, p. 149).

The size at sexual maturity for the male sperm whale in the Southern Hemisphere was first estimated by Matthews (1938, p. 144) as 12 meters. In the Azores, Clarke (1956*a*, p. 442) arrived at a figure of about 9.5 meters. In the waters off Japan, most males reach sexual maturity at about 12 to 13 meters (Nishiwaki and Hibiya, 1951, p. 161; Nishiwaki, 1955, p. 148; Nishiwaki *et al.*, 1955, p. 42), and the testes of all males in the North Pacific above about 14 meters contain active spermatozoa. In the antarctic, the length of males of which 75 per cent had testes weights of more than 1.5 kg was about 13.5 meters, according to Nishiwaki (1955, p. 148), who concluded that there may be a difference in size at maturity between the males of the Northern Hemisphere and those of the Southern Hemisphere.

The presence of the female does not influence male testis size. Nishiwaki *et al.* (1955, p. 44) compared testis size of harem bulls with that of isolated bulls and found no significant difference.

Sexual cycle.—Matthews (1938, p. 132) was unable to show a sexual season for the male sperm whale, but Clarke (1956*a*, p. 443; 1956*c*, pp. 271 ff.) states that histological evidence does point to a prolonged sexual season (in the Azores), beginning before June and extending beyond October.

Information regarding the sexual cycle of the female has been worked out in some detail. The gestation period is sixteen months (Matthews, 1938, p. 136; Clarke, 1956*a*, p. 443) or seventeen months (Mizue and Jimbo, 1950, p. 128). Parturition occurs from May to November in the Azores, with a peak from July to September (Clarke, 1956*a*, p. 443). Slijper (1962, p. 116) postulates a parturition period lasting from May to August in the North Pacific. Off the coast of California, parturition is somewhat later, occurring from August to December (Rice, 1963). In the Southern Hemisphere parturition occurs from December through April, with a peak in February (Matthews, 1938, p. 138). Here there is an approximate reversal of the seasons found in the Northern Hemisphere.

Lactation lasts for thirteen months (Clarke, 1956*a*, p. 443), which accounts for Bennett's (1840, II, 179) observation that he observed suckling calves the entire eight months of his cruise. The long nursing period is usually, but not always, followed by a seven-month anestrus (Clarke, 1956*a*), contrary to Matthews' (1938, p. 134) original opinion that no resting period occurred between the end of lactation and the next conception.

Matthews (1938, p. 141) postulated a diestrous cycle with about four ovulations at each estrus. Further data are needed.

The lactation period may sometimes overlap the next pregnancy, as pregnant lactating females are sometimes taken (Matthews, 1938, p. 134; Clarke, 1956*a*, p. 443). The seven-month anestrus, therefore, does not always occur.

In Japanese waters, it has been established that 25 to 33 per cent of the females are pregnant (Ohsumi *et al.*, 1963, p. 29).

The mean length at birth of fetuses examined in the Azores was 3.92 meters (Clarke, 1956*a*, p. 443). The maximum length of a fetus examined in Japanese waters was 4.3 meters (Mizue, 1950, p. 117).

The mean length of the calf at weaning is 6.7 meters (Clarke, 1956*a*, p. 443).

Tail presentation occurs at parturition in the sperm whale (Slijper, 1956, p. 23; Ash, 1962, p. 15), as in all other cetaceans for which information is available (Slijper, 1956).

Breeding season.—A definite breeding season for the sperm whale has been successfully demonstrated by plotting fetal lengths against time of year of capture. The season is extended and is different in the Northern and Southern hemispheres. For the Southern Hemisphere, Matthews (1938, p. 137) obtained data at Natal which indicate a seven-month pairing period mainly concentrated in the five months from August through December, with the peak in October. For the Northern Hemisphere, Clarke (1956*a*, p. 443) found the pairing season in the Azores to be from January to July, with the peak extending from March through May. The pairing period in Japanese waters is in March (Mizue and Jimbo, 1950, p. 127). The peak breeding season in these regions, then, occurs in the spring and early summer in each hemisphere. Off the California coast the breeding season is somewhat later, extending from April to August. Colder water temperature could account for the delay. In the Southern Hemisphere, Matthews (1938, p. 132) found active spermatozoa in males from January through November.

Breeding area.—The young are both conceived and born in the areas of the harem bands, concentrated between latitudes 40° N. and 40° S. (Jonsgård, 1960, p. 289). Matthews' (1938) evidence suggests that males that are unable to secure harems in the spring migration continue to migrate southward toward the pole, while the successful males remain with the herd over the spring and summer months and impregnate the females. Matthews (1938, p. 159) and Allen

(1942, p. 492) believe, however, that copulation occurs during the course of the migration itself, but their data indicate to us that conception occurs only after the feeding grounds have been reached. Colnett (1798, p. 147) also reported that copulation was common on the Galápagos grounds.

Copulation.—Copulation has been observed in both the vertical (Bennett, 1840, II, 179; Slijper, 1962, p. 353) and horizontal (Ruspoli, 1955) positions. The duration observed on the latter occasion was about ten seconds.

Social Facilitation

Social facilitation is defined as activity by an individual which stimulates the immediate performance of the same activity by its neighbors (Crook, 1961, p. 135). We have been impressed by this behavior in our observations of captive individuals of *Tursiops truncatus* and *Lagenorhynchus obliquidens*. Social facilitation apparently also exerts a strong influence on the behavior of sperm whales, particularly in times of alarm.

Bennett (1840, II, 173) noted that at times the herd would leap, descend, rise, and even blow nearly in unison. Birkeland (1926, p. 147) recorded a group of sperm whales that dived together as if on signal, remained under for 50 minutes, then surfaced together. Rice once saw four males, each approximately 13.5 meters long, surfacing and diving synchronously at intervals of 14 to 22 minutes. In diving, the animals apparently adjust to the diving abilities of the smallest individuals, for large mixed herds remain submerged for only 10 or 15 minutes, even though solitary animals may remain under for as long as an hour (Millet, 1924, p. 5). Rice once timed three successive dives by a large male at 57, 62, and 50 minutes.

A herd also may swim in perfect rows, side to side. Beane (1905, p. 170) described one school of at least fifty individuals swimming about 33 meters apart, "like soldiers on parade." Tripp (1938, p. 237) used the expression, "lined up almost as soldiers," in describing the flight of twelve frightened sperm whales, which also spouted in unison as they fled. Bennett (1840) also reported that schools sometimes swim in rows (I, 294) and retreat in rows (II, 173).

Nishiwaki (1962, p. 398 and fig. 6) observed a group of at least ten sperm whales gathered at the surface, head to head, "like a marguerite flower," and splashing their tail flukes. Captain Loyd Newton described (to Rice) similar behavior by sperm whales off Peru.

Alarm in one member of a school is usually communicated immediately to other members of the school (Brown, 1887, p. 266). The school may then flee the area, or, if the alarmed individual has been injured and is a female or a calf, the school may gather around and remain with the injured member (see contribution to this volume by Caldwell and Caldwell).

Long-distance communication of alarm is typical of sperm whales and has been noted by whalemen. Sound production is the most likely method by which the alarm is communicated, although it could be conveyed for short distances by visual signals. Macy (1877, p. 114) reported that on one occasion a sperm whale bull, when alarmed, raised its head in the air, and alarm was instantly communicated to the other members of the school. Andrews (1916, p. 234) observed, conversely, that when a large school of sperm whales is attacked, the center whales are unaware of the slaughter going on at the rim.

As pointed out by Gilmore (1959, p. 15), the sperm whale, like some other cetacean species, strands in groups. Group strandings of juvenile males have been reported (Gilmore, 1957), as well as of harem bands of females, young males, and calves (Oliver, 1922, p. 566). Social cohesion and facilitation, therefore, also are important factors among juvenile males, despite the apparently looser organization of their herds and the fact that they presumably do not "stand by" injured members of the group, as do the females. Ed Holloway, a sperm whaler who operates near California and Vancouver Island, reported (to Rice) seeing two tightly organized schools of four and six male sperm whales, each animal approximately 13 meters in length, off the coast of California on April 24, 1963. Holloway admitted, however, that it was the only occasion in fifteen years of whaling experience that he had seen tight schooling behavior in males. Later the same day Rice encountered the same school of four (after two animals had been killed), and affirmed that the remaining two animals were still tightly schooled and were sounding and surfacing together at intervals of fourteen to twenty-two minutes.

AGONISTIC BEHAVIOR

Under the term "agonistic behavior" are included all the responses that animals give when they are either inflicting injury or are in danger of being injured (Scott, 1958, p. 71). Such responses may be aggressive or defensive fighting, escape behavior or passivity (*ibid.*). Observations on the external manifestations and causes of all these reactions are available for the sperm whale.

When alerted to danger, the sperm whale may raise its head and stand upright with the entire head out of water, so that the eyes are clear of the surface, and then slowly mill around in a complete circle (Ashley, 1942, p. 81). This gesture is known as "pitch poling" (*ibid.*). Observations of similar visual inspection were also recorded by Spears (1908, p. 180) and Hopkins (1922, p. 194). Norris and Prescott (1961, p. 345) have reported very similar behavior by the Pacific pilot whale, *Globicephala scammoni*, when a "loafing group" was approached by a boat. The pilot whales "stood" in the water and inspected the approaching boat visually. Rice has seen a sperm whale, when being chased for marking purposes, raise its head diagonally at an angle of about 30 degrees above the horizontal, so that its eyes were above the surface. The whale may also stop breathing and lie motionless (Bennett, 1840, II, 176), or sweep the flukes back and forth in an exploratory manner (*ibid.;* Scammon, 1874, p. 75; Hopkins, 1922, p. 279).

Older whales are normally not so cautious as young ones (Beale, 1839, p. 51). Earlier whalemen, however, exercised great care in approaching all sperm whales, as stealth rather than superior speed was the important factor in making the catch. They approached the whale either from the direct front or the direct rear, where they could not be seen, and were as quiet as possible. The sound of an oar touching a boat could put an entire school to flight (Haley, 1948, p. 73). The minute click of an underwater camera reportedly was sufficient to cause a sperm whale to change course (Haas, 1959, p. 177).

Flight is the usual reaction of sperm whales to danger. Despite their great size and strength, they have reportedly been put to flight by schools of dolphins, with their vigorous swimming and jumping activities (Bennett, 1840, II, 176; Murphy, 1947, p. 95).

Three flight reactions are described in the literature: (1) rapid swimming from the danger area; (2) sounding by throwing the flukes into the air and diving perpendicularly; and (3) a rapid horizontal settling. When fleeing, the whales may swim fast, blow often, and not dive deeply. Sounding is the most commonly reported escape reaction (Wilkes, 1845, p. 496; Nordhoff, 1895, pp. 220, 227; Hopkins, 1922, pp. 306, 319, 330; Watson, 1929, p. 16; Haley, 1948, p. 269; Clarke, 1954*b*, p. 330), contrary to Scholander's (1940, p. 102) statement that the sperm whale rarely dives after being harpooned. The rapid horizontal settling is referred to least frequently (Scammon, 1874, p. 75; Hopkins, 1922, p. 194; Davis, 1926, p. 187; Tripp, 1938, p. 194).

Sometimes, when a lone bull sounds, he is not seen again (Hopkins, 1922, p. 281), indicating an ability to swim long distances underwater.

One puzzling aspect of flight behavior is the frequently noted fact that sperm whales, when running, flee to windward (Olmstead, 1841, p. 79; Browne, 1846, pp. 117, 295; Hazen, 1854, p. 72; Hopkins, 1922, pp. 147, 197, 214; Murphy, 1947, p. 99; Haley, 1948, pp. 73, 269). Haley (1948, p. 73) has also pointed out that the whales, if the air is calm, usually turn to the direction from which the wind blew last, and never deviate by a compass point from their flight in this direction. On one occasion a frightened school ran to leeward, but this action was commented upon as being contrary to usual practice (Nordhoff, 1895, p. 106). If, as it would seem, odontocetes have no sense of smell (Slijper, 1962, p. 236), it is difficult to explain the adaptiveness of this behavior; we question the suggestion that it is vestigial, left over from the earlier cetaceans who retained the sense of smell (Slijper, 1962, p. 237).

Frightened sperm whales have an explosive expiration (Davis, 1926, p. 184; Haley, 1948, p. 103), similar to the one we have observed in excited captive *Tursiops truncatus.*

Although flight is the usual reaction to stress, aggressive reactions have been reported on many occasions. Andrews (1916, p. 177) expressed the opinion that, except for gray whales (*Eschrichtius glaucus*) defending their young, the sperm whale is probably the only whale that attacks deliberately. The bull sperm whale is usually implicated in these unprovoked attacks, such as the one on the bark *Kathleen* in 1902 (Anonymous, 1938, p. 21) and the one on the whaleship *Essex* (Chase, 1963, p. 19; Stackpole, 1953, p. 45). The large whaleship *Parker Cook* was rammed twice by a bull sperm whale (Starbuck, 1878, pp. 123 f.). The animal that attacked and sank the *Ann Alexander* was undoubtedly a sperm whale, for it was captured two months later still carrying the *Ann Alexander*'s irons, and its teeth were used for scrimshaw (Sawtell, 1962, p. 83). Customarily the only whale teeth scrimshawed were those of the sperm whale, and members of this species also are the only toothed whales capable of such an act. Sperm whales also have been known to take the initiative and attack as whaleboats approached (Haley, 1948, p. 76; Stackpole, 1953, p. 451).

Although frequently allowing themselves to be slaughtered impassively, harpooned sperm whales have on many occasions secured their release by aggressive maneuvers. In fighting, the chief weapons of offense are the toothed jaws in biting, the head in ramming, and the flailing flukes. The jaw is exceedingly maneuverable and can be dropped far down or swung from side to side (Scammon, 1874, p. 82). Any object 5 meters away on either side is in danger from a sperm whale's jaw (Ashley, 1942, p. 81). The lower jaw can be extended in a vertical plane at right angles to the body, or nearly so (Hammond, 1901, p. 174; Hopkins, 1922, p. 316). The sperm whale's usually reported method of attack on a small boat is to turn over on its back or side and approach belly up, with the jaw agape (Bennett, 1840, II, 176, 217; Scammon, 1874, p. 82; Brown, 1887, p. 261; Beane, 1905, p. 338; Hopkins, 1922, p. 338; Ferguson, 1936, pp. 41, 79; Ashley, 1942, p. 82). The species has also been reported to attack with the jaws, from beneath boats (Hammond, 1956, pp. 28 ff.), or by approaching belly down with the head held high out of the water and the jaw held open and horizontal to the surface of the water (Hazen, 1854, p. 80). Whitecar (1860, p. 344) noted only that a whaleboat was grasped in the jaws. The jaw is powerful, and whaleboats have been bitten cleanly in two by sperm whales (Beane, 1905, p. 148; Hopkins, 1922, p. 316; Cook, 1926, pp. 9 f.)

When angered, sperm whales may continue to bite at the debris of boats they have destroyed (Scammon, 1874, p. 79; Brown, 1887, p. 261; Hopkins, 1922, p. 151; Cook, 1926, pp. 9 f.). Uninjured whales in the vicinity of destroyed boats have been known to bite at the debris (Bennett, 1840, II, 217). On one occasion when a whale was harpooned, an uninjured whale remained and with its flukes destroyed a whaleboat (*ibid.*, p. 216).

Apparently the jaw clap characteristic of angry captive *Tursiops truncatus* (see McBride, 1940, p. 25; McBride and Hebb, 1948; Wood, 1954, p. 123; Tavolga and Essapian, 1957, p. 13) is also characteristic of angry sperm whales. Loud jaw clapping at such times has been reported (Beane, 1905, p. 149; Hopkins, 1922, pp. 311, 316; Ferguson, 1936, pp. 41, 79), and the whale that attacked the *Essex* also clapped its jaws between attacks (Chase, 1963, p. 20). The jaw clap is of such force, it has been said, that it can be heard for two or three miles (Shaler, 1873, p. 3).

One method of distracting an angry sperm whale's attention from a whaleboat was to throw a cask overboard which the whale could then attack instead of the boat. On one occasion the cask reportedly was rammed with the head (Hopkins, 1922, p. 338). It is obvious that the injured animal had no idea where the actual danger lay, but struck at any foreign object in its vicinity.

Whales have frequently attacked whaleboats by ramming them with the spermaceti case (Bennett, 1840, I, 265; Beane, 1905, p. 149; Hopkins, 1922, p. 316; Murphy, 1947, p. 29; Haley, 1948, p. 76). The bull sperm whale that made the unprovoked attack upon the *Essex* also rammed with its head (Chase, 1963, p. 19). In one instance Brown (1887, p. 261) reported that the bones of a whale's head were fractured by a head-on attack on a whaleship, and splinters were later found in the head of the whale that attacked the *Ann Alexander* (Sawtell, 1962, p. 83). A whale that attacked one whaleboat with its jaws attacked a second boat moments later by ramming with its head (Hopkins, 1922, p. 316), indicating variable behavior by the same animal.

The sperm whale is said to be dangerous at both ends (Brown, 1887, p. 263). Although the jaws and the head are the chief weapons of aggression, the flukes are also employed effectively (Beale, 1839, p. 51; Bennett, 1840, II, 214, 216; Nordhoff, 1895, p. 161; Bullen, 1899, p. 119; Stackpole, 1953, p. 45). According to Bennett (1840, II, 157), when the flukes are used in offense, they are turned contrary to the direction of the object aimed at, and the blow is inflicted by the force of the recoil. On the same occasion a whale may vary its attack from flukes to jaws (Bullen, 1899, p. 119).

A harpooned whale that escaped reportedly returned to the attacking whaleboat and capsized it (Nordhoff, 1895, p. 227).

Young bulls are said to be the most vigorous in defense (Bennett, 1840, II, 206; Scammon, 1874, p. 77; Murphy, 1947, p. 99), contrary to Slijper's (1962, p. 29) statement that they allow themselves to be slaughtered impassively. Bennett (1840, II, 206) added that old females may also be dangerous.

Descriptions of fights between bull sperm whales are available in the older literature. The most detailed account was given by Hopkins (1922, pp. 326 ff.). A bull, a cow, and an injured calf were seen one day and followed overnight in an attempt at capture. The next day the three animals joined a school of about a hundred smallish cows and two or three bulls. When the approaching bull attempted to join the herd, he was attacked by one of the established bulls, which rolled over on its back and attacked with its jaw, with the jaw protruding from the surface. Large pieces of blubber and flesh were taken out. Both bulls then withdrew and again charged at full tilt. They locked jaws and wrestled, each seeming to try to break the other's jaw. Great pieces of flesh again were torn from the animals' heads. Next they either withdrew or broke their holds, and then charged each other again. The fight was even more strenuous this time, and little could be seen because of the boiling spray. The charge and withdrawal were repeated two or three times before the water quieted, and then for a few seconds the two could be seen lying head to head. The smaller bull then swam slowly away and did not attempt to rejoin the cows. He was allowed to withdraw without further evidence of aggression by the victor. Both bulls seemed to be in distress, and the larger one was apparently unable to move its jaw properly. A whaleboat was dispatched, and the larger bull was captured. The jaw had been broken and was hanging by the flesh. Many teeth were broken and there were extensive head wounds.

Shaler (1873, p. 2) and Hopkins (1922, p. 318) also mentioned males that fought with their jaws, and Shaler (1873, p. 2) reported that one had been taken with the lower jaw torn almost completely off. The *New Bedford Gazette* of 1837 (Spears, 1908, p. 192) described a fight in which the animals charged each other with jaws extended and tore much of the flesh from each other's heads. Tooth marks were left on other parts of the body as well. The jaw of one of the combatants had been broken off and was hanging by the flesh, and the jaw of the other was displaced and many teeth were broken.

On a recent Russian expedition sperm whale fights were observed twice (Zenkovich, 1962, p. 200). Such fights undoubtedly account for the frequent reports that captured male sperm whales have scars or deep scratches on the skin, corresponding to tooth marks (Shaler, 1873, p. 2; Hopkins, 1922, p. 318; Bennett, 1932, p. 67; Lillie, 1955, p. 92; Slijper, 1962, p. 198; and observations by Rice). When fresh, these tooth marks resemble ulcerous sores (Olmstead, 1841, p. 141). Broken teeth found in sperm whales may also be the result of combat (Davis, 1926, p. 171). A sperm whale with a broken but healed jaw has been captured (Murphy, 1947, p. 118). Reports of broken jaws must, however, be differentiated from a type of deformity of the lower jaw which regularly afflicts a small percentage of sperm whales. In animals so afflicted the jaw is curved or even spiraled, but there is no evidence of a break (Murie, 1865; Clarke, 1956*c*, p. 255; Nasu, 1958). Ash (1962, p. 67) clearly distinguishes between this twisted jaw, which he has seen on two occasions, and one example of a broken jaw.

Clarke (1956*c*, p. 249), Nishiwaki *et al.* (1958, p. 149), and Rice have observed the interesting point that the teeth do not pierce the gums until the animal reaches sexual maturity. This time comes long after weaning is over and squid are being taken successfully. It may be, therefore, that teeth are more a secondary sexual characteristic than a mechanism for food getting. In relation to this point, it should be noted that the specialized teeth of ziphiids, so far as is known, are functional only in adult males. When Tomilin (1955, pp. 6 f.) inspected the mouths of 231 male and 124 female common dolphins (*Delphinus*) in May, he found tooth injuries restricted to the males. The number of tooth injuries increase markedly in June during the height of the pairing season. No missing teeth were found in immature males. Of 26 sperm whales examined (number of each sex not stated), Clarke (1956*c*, p. 251) found broken teeth in 4 males, but in only 1 female. Davis (1926, p. 171) observed that old bull sperm whales frequently have broken or shattered teeth. Rice noted broken teeth in 3 of 122 males examined, and in none of 42 females.

In addition to flight or fight, sperm whales occasionally manifest a third reaction to danger. They may crowd together "still and trembling," (Bennett, 1840, II, 176) or "like frightened sheep" (Bullen, 1899, p. 106). Kingsley (1884, p. 193) also noted that they sometimes lie paralyzed, even when struck. Although such behavior seems maladaptive in the sperm whale, which is capable of escape by deep diving, Tomilin (1955, p. 5) listed it as a defense reaction of *Delphinapterus leucas* and *Eschrichtius glaucus* against killer whales (*Orcinus orca*); the hunted animal attracts less attention from the predator if it is motionless.

PLAY BEHAVIOR

We have been unable to locate or to formulate a completely satisfactory definition of the difficult concept of play. For purposes of this paper, therefore, we include any behavior that apparently is performed for the sake of the activity itself, rather than for any observable effect it may have upon the environment, and behavior that cannot be shown to contribute immediately to any of the recognized internal drives that maintain life. The two types of sperm whale behavior most frequently referred to which come under this definition are breaching and lobtailing.

Breaching is accomplished by throwing the body vertically out of the water. In falling back into the water, the sperm whale falls sideways (Darwin, 1882, p. 223; Ashley, 1942, p. 81) or on the belly (Ashley, 1942, p. 81) with a sound that reverberates like a broadside of guns (Darwin, 1882, p. 223). The flukes may be shaken when returning to the water (Olmstead, 1841, p. 135).

The height to which sperm whales can leap has been discussed by Davis (1926, p. 173), who never saw them leap completely clear of the water, as reported by Beale (1839, p. 48). Bennett (1840, II, 216), however, made the observation that the animals seemed to suspend several meters above the water, and Ashley (1942, p. 81) once saw a sperm whale clear the water so that the setting sun was framed under the hurtling form. According to Davis (1926, p. 398), two ship captains reported seeing sperm whales completely clear the water on breaching, and Hopkins (1922, p. 56) affirmed that they can clear the water. This feat is exceptional, however, and the more usual breach is apparently of a lesser degree (Bennett, 1840, II, 173), with the flukes not clearing the water (Darwin, 1882, p. 223; Edwards and Rattray, 1956, p. 150). The same whale may breach three or four times in succession (Beddard, 1900, p. 203).

Although breaching is most probably play behavior similar to that seen in the smaller cetaceans (Norris and Prescott, 1961, p. 330), it has also been suggested that sperm whales may conceivably rid themselves of parasites or remoras in this way (Beale, 1839, p. 48).

A sperm whale is lobtailing when it places itself perpendicularly in the water, head downward, and swings its tail from side (Davis, 1926, p. 182), bringing the flat of the flukes against the water. When the flukes strike the water, the sound, it has been said, can be heard for great distances (Ashley, 1942, p. 81). It has been compared to the sound made by a "great gun" (Hopkins, 1922, p. 56) or a cannon (Millet, 1924, p. 20). Ashley (1942, p. 80) observed the behavior while sperm whales were feeding or at play, and an entire school may simultaneously engage in lobtailing (Bullen, 1899, p. 110). When lobtailing, a large sperm whale may throw its flukes as far as 10 meters or more out of the water (Ashley, 1942, p. 81).

Although it has been suggested that lobtailing may be an emotional manifestation of alarm and therefore a means of communication (Hopkins, 1922, p. 61), schoolmates of lobtailing sperm whales often show no reaction to the sound (Hammond, 1901, p. 153; Hopkins, 1922, p. 61; Davis, 1926, p. 182; Ashley, 1942, p. 81). The sound must therefore be perceived according to the context in which it is made. Norris and Prescott (1961, p. 322) observed the Pacific bottlenose dolphin, *Tursiops gilli*, lobtailing in three different situations: in alarm, while feeding, or just before a deep dive.

Although sperm whales do not come close inshore, observations of their activities on the high seas sound suspiciously similar to reports of surf-riding by the smaller cetaceans (Caldwell and Fields, 1959; Norris and Prescott, 1961, p. 300) and by the gray whale (Caldwell and Caldwell, 1963). While cruising near Three Kings Islands off New Zealand in heavy seas, Haley (1948, p. 55) made the following observation: "Casting our eyes in that direction, we could see twenty or thirty good sized whales tumbling about when the big seas would catch them and almost turn them over. Sometimes one could be seen on the crest of a wave. As it broke he would shoot down its side with such speed a streak of white could be seen in the wake he made through the water. . . . I have never seen whales at play before or since."

There is a report (Slijper and Utrecht, 1959, p. 114; Slijper, 1962, p. 187) of a sperm whale playing with a plank; the animal was diving back and forth under the plank, and not relinquishing it even though a ship was approaching. Nishiwaki (1962, fig. 3) presents an illustration of a sperm whale playing with a piece of timber while five other whales give chase.

SWIMMING BEHAVIOR

In ordinary swimming, the movement of the flukes is a straight up-and-down stroke (Ashley, 1942, p. 81). From motion pictures made aboard the *Calypso,* Slijper (1962, p. 101) concluded that the tail beats almost vertically about a point near the vent.

On the downstroke the flukes are tilted upward, and on the upstroke they are tilted downward (Ashley, 1942, p. 81). This description of the curved propellant stroke in sperm whales is similar to that given by Slijper (1962, p. 101 and fig. 61) for a small porpoise, and by Parry (1949*a*, *b*) for *Tursiops truncatus.* Ashley (1942, p. 81) also noted a slight sideways motion of the flukes, similar to the motion of a scull, when sperm whales were swimming slowly. He (*ibid.*) added that, when the whale is swimming slowly, on one stroke the tail approaches a boat, and on the next stroke it is turned away. This flexibility allows for quick turns and steering (Slijper, 1962, p. 102). Bennett (1932, p. 44) also mentions the possibility of a partly screwlike motion of the tail flukes which is difficult to detect. The semantics here are poorly defined, but it is probably this motion that Parry (1949*a*, *b*) does not believe exists in *Tursiops truncatus* from the moving pictures he has viewed, or in *Balaenoptera physalus* or *Phocoena phocoena* from anatomical evidence. In normal swimming the flukes do not break the surface (Murphy, 1947, p. 91).

The sperm whale's head is held above the water when it is swimming rapidly (Bennett, 1840, II, 172; Ashley, 1942, p. 81), and pitches up and down with the beat of the flukes (Ashley, 1942, p. 81). Hammond (1901, pp. 126, 156) described swimming as occurring in peculiar lunging leaps, in a school of bulls. He noted that the head was thrust 10, 12, or 15 feet out of the water, and then was followed by the body.

Calves accompany and keep up with the school as soon as they are born (Bennett, 1840, II, 179). Norris and Prescott (1961, p. 301) described a form of assisted locomotion in *Lagenorhynchus obliquidens*; a smaller animal swims by a larger one in such a position that it does not require much expenditure of energy to maintain a fast rate of speed. The increased energy necessary to propel the two animals is furnished by the larger animal. Such an arrangement in sperm whales may be the factor that enables the young to maintain the speed of the school.

Estimates of swimming speed in sperm whales fall into three rough categories: normal speed, speed when alarmed, and speed after being harpooned. There is a fair degree of correlation in whalemen's estimates of speed in each of these categories.

Observations of normal speeds vary from 2.5 to 4.3 knots (Scammon, 1874, p. 76; Clark, 1887, p. 211; Andrews, 1916, p. 232; Davis, 1926, p. 185; Sapin-

Jaloustre, 1953, p. 238). Schools of fifty or more sperm whales rarely swim at more than 4 to 5 knots (Murphy, 1947, p. 46). In one marking experiment, the average traveling speed of two sperm whales, a male and a female each less than 12 meters in length, was 2.4 knots for a four-day period (Kawakami and Ichihara, 1958, p. 289). There is one observation (Hopkins, 1922, p. 315) of a whale that was not alarmed but swam in a "businesslike manner" at 5 or 6 knots. Slijper (1962, p. 112) estimated a much higher average, 10 knots, for sperm whales, but his figure is so much higher than others that his observations must have included periods when the whale was under stress.

The sperm whale increases its swimming speed when frightened or alarmed. Estimates of speed under these circumstances range from 6 to 12 knots (Beale, 1839, p. 39; Bennett, 1840, II, 172; Andrews, 1916, p. 232; Davis, 1926, pp. 185, 398; Sapin-Jaloustre, 1953, p. 238).

The sperm whale can achieve even higher speeds for brief periods when under the extreme stress of being harpooned. Then it can *briefly* tow a whaleboat and a full complement of men at speeds estimated at from 10 to 21 knots (Bennett, 1840, II, 172; Brown, 1887, p. 265; Hopkins, 1922, pp. 71, 194; Davis, 1926, p. 398; Tripp, 1938, p. 220; Clarke, 1954*b*, p. 331). In one incident described by Hopkins, a harpooned sperm whale pulled a boat for four or five hours, first at 12 knots, then at 10, and finally at a lower speed.

When swimming normally, sperm whales follow a direct course and maintain the same speed for hours. Ship captains, it has been reported, have gauged the speed and direction of a sperm whale during the day, followed the same course and speed throughout the night, and were still within sight of the pursued animal the next morning (Hopkins, 1922, pp. 326 ff.; Davis, 1926, p. 182). Scammon (1874, p. 76) pursued one sperm whale that maintained a direct course for five hours.

DIVING AND RESPIRATION

Diving and respiration are reviewed together here because they are so intimately related in the sperm whale and because deep-diving ability depends to so large an extent upon oxygen storage and metabolism.

Sperm whales are among the longest and deepest divers of all cetaceans, possibly being exceeded only by the bottlenose whale, *Hyperoodon* (see Scholander, 1940, p. 79), and *Berardius* (see Matsuura, 1943). The limits of duration and depth of the dive are determined largely by the size of the individual. The larger sperm whales dive for longer periods of time. One of this large class was reported to have remained under for as long as 90 minutes (Bennett, 1840, II, 175). Other top estimates of lengths of dives are 80 minutes (Beale, 1839, p. 43; Clark, 1887, p. 212), 75 minutes (Scammon, 1874, p. 76; Clarke, 1954*b*, p. 328), 60 to 70 minutes (Hopkins, 1922, p. 55), and 65 minutes (Beane, 1905, p. 125).

Rice observed an individual that remained down for 62 minutes. A 60-foot sperm whale, which is one of the largest bulls, was reported usually to dive for about an hour (Ashley, 1942, p. 76). Bennett (1840, II, 175) also noted that the largest whales remain under for about an hour, and Beale (1839, p. 43) recorded a duration of from 60 to 80 minutes for dives by large bulls.

For each minute spent diving, a large bull respires approximately once. The whalemen's rule of thumb was that a 60-foot sperm whale weighing nearly 60 tons stayed down 60 minutes and spouted 60 times (Ashley, 1942, p. 76). Scammon (1874, p. 76) observed one whale that dived for 55 minutes and spouted 55 times. Another dived for 65 minutes and spouted 50 times (Beane, 1905, p. 125). Fifty, 60, or 70 breaths are not unusual (Davis, 1926, p. 176). If this pattern is interrupted and the number of respirations is reduced for any reason, the whale cannot remain submerged so long on the next dive. The whale must either have its "spoutings out" or rise early to blow (Beale, 1839, pp. 43, 181). One bull remained at the surface breathing approximately 10 or 11 minutes taking 60 to 70 breaths (*ibid.*, p. 43). Scammon (1874, p. 76) gave a figure for a large bull of 12 minutes with 60 to 65 respirations, as each cycle of expiration-inspiration requires 10 to 12 seconds. Hopkins (1922, p. 55) estimated 11 seconds per respiration (expiration-inspiration). The spout itself averages about 3 seconds (Ashley, 1942, p. 69).

The pattern of diving and respiration in large bulls is extremely constant. As these animals also usually swim a direct course when moving, the time and place of surfacing could often be predicted by whalemen with considerable accuracy (Andrews, 1916, p. 231). Davis (1926, p. 182) reported that a ship captain, following a bull for twelve hours, found that neither the length of the dive nor the number of spouts nor the direction of course varied at all during this period. Scammon (1874, p. 76) followed a whale for five hours, during which time it did not vary in the length of its dive or in the number of spouts. A sperm whale that Scholander (1940, p. 79) followed for an entire day submerged for about 57 minutes during each dive.

Young or female sperm whales do not remain down so long, they respire more frequently for each minute spent in diving, and they do not demonstrate the same degree of regularity. Females remain below for about 20 minutes and at the surface for about 4 minutes, breathing 30 to 40 times (Beale, 1839, p. 43; Scammon, 1874, p. 76). The shortest duration of any dive clocked by Clarke (1954*b*, p. 328) was 5 minutes.

Sperm whales surface in a horizontal position, so that the hump or top of the head is the first part of the body to emerge (Scammon, 1874, p. 75; Ashley, 1942, p. 81). As soon as the blowhole clears the water, the breath is released (Ashley, 1942, p. 81). This observation of the time of release of the breath agrees with Tomilin's (1955, p. 2) experiments, which point toward the questionable idea that breathing in cetaceans is an unconditioned reflex that closes the blowhole when water touches it. There are references, however, to sperm whales "snapping their spout holes" when fighting (Hopkins, 1922, p. 311; Davis, 1926, pp. 236, 355), so another factor may be involved in addition to exposure to air or contact with water.

The first blow after a sperm whale rises is an explosive blast that may be heard for nearly 250 meters (Clarke, 1954*b*, p. 328). Succeeding spouts are less forceful, but even the final spout is visible (Ashley, 1942, p. 69). The spout is moist (Ashley, 1942, p. 70) and fetid, and has a burning effect on the human skin (Bennett, 1840, II, 173). It has been suggested that nitrogen-charged foam is expelled at expiration (Fraser and Purves, 1955). The air sinuses of sperm whales, compared with those of baleen whales, contain unusually large amounts of a very stable mucous-oil foam. We question the statement that there is no sound of inspiration (Bennett, 1840, II, 174; Davis, 1926, p. 182).

The height of the spout has been estimated at 6 to 8 feet by Bennett (1840, II, 174), not more than 9 or 10 feet by Hazen (1854, p. 79), and not more than 10 or 12 feet by Ashley (1942, p. 69). Slijper (1962, p. 117), however, states that the blow of the sperm whale is much higher, 16 to 25 feet, and that the height of the spout is underestimated because an optical illusion is created by its forward oblique angle (Slijper, 1962, p. 119). As Slijper (p. 117) pointed out, however, the height of the spout is largely a function of the size of the animal. The spout of a baby sperm whale is thin and scarcely more than a foot in height (Tripp, 1938, p. 236).

Sperm whales sound by lifting the forward part of the body a few feet into the air, giving a strong spout, rounding the back in a high arch, and descending steeply (Davis, 1926, p. 182). Sometimes, however, when disturbed, they may simply settle (Bennett, 1840, II, 174).

It has long been believed by whalemen that sperm whales could descend to depths as great as some 1,500 meters (Beale, 1839, p. 164), for that much line was taken out and the whales appeared to dive vertically and to return straight at the boat. Many people, however, judged this estimate to be an error, believing that such pressures would kill the animal. The first verification that sperm whales might actually dive to such depths appeared in 1932 in a newspaper account of a bull sperm whale approximately 14 meters long which was hoisted from a depth of 988 meters, where it obviously had become entangled alive in a submarine cable (Laurie, 1933, p. 369; Kellogg, 1938, p. 666; Heezen, 1957, p. 112). Heezen (1957) reported several other cases of whales entangled in submarine cables. Two of these (cases 12 and 14) were undoubtedly sperm whales (Heezen, 1957, figs. 4–6). In one instance the entangled jaw was brought up from a depth of 620 fathoms (1,145 meters). From the entanglements, Heezen suggested (p. 110) that the whales swam along the bottom with the lower jaw agape in search of food.

The rate of respiration is dependent upon the amount of exertion the animals have made and the oxygen deprivation they have undergone. As noted previously, when returning from a dive the whale respires once every ten or twelve seconds for several minutes (Scammon, 1874, p. 76). When swimming leisurely at the surface, they respire every two or three minutes, but when swimming at high speed the rate of the blow increases to once each minute (Slijper, 1962, p. 115). This breathing is similar to "panting" in terrestrial mammals (*ibid.*, p. 125).

Female and young male sperm whales reportedly take out only one and a half tubs of line (Bennett, 1840, II, 206), or 300 fathoms (554 meters) (Jenkins, 1921, p. 216). They undoubtedly do not dive so deep as the bulls, which are recorded as taking out three tubs, or 600 fathoms (1,108 meters), of line (Chatterton, 1926, p. 73). Hopkins (1922, p. 55) noted that sounding whales frequently took out a kilometer of line, or sometimes more, straight down, and came up again straight to the boat.

Physiological adaptations to deep diving have been reviewed by Kellogg (1938), and more recently by Slijper (1962, pp. 124 ff.). The adaptations are many and include reduction of lung capacity; increase in oxygen capacity of blood, muscle, and other tissues; and a postulated transfer to a predominantly anaerobic phase of glycogen decomposition during the dive (Slijper, *loc. cit.*). Many other adaptations, however, are also involved. Interested readers are referred to the excellent review of the subject by Slijper, who also summarizes the literature. The only possibly helpful reference omitted by Slijper from this section of his book, although he included it under metabolism, is the study by Geiling (1935). Geiling postulated (p. 133) that the high ratio (12:1) of pressor to oxytoxic material in the posterior pituitary enables sperm whales to dive deeply, inasmuch as injection of pituitary extract into animals reduces oxygen consumption and slows the blood flow.

FOOD AND FEEDING

Although the early whalemen did not often examine the stomach contents of the animals they caught, except sometimes in search of ambergris, they were aware that the main item of diet was squid (Colnett, 1798, p. 171). Bennett (1840, II, 175) also recognized that rock cod and sharks were occasionally an adjunct to the diet, and Bullen (1899, p. 342) mentioned snapper and barracuda. Whalemen were so knowledgeable about the diet of sperm whales because an animal frequently vomited its stomach contents when attacked (Bennett, 1840, II, 175; Shaler, 1873, p. 3; Brown, 1887, p. 264; Buchanan, 1896, p. 224). According to Beale (1839, p. 34) and Cheever (1850, p. 113), pieces of squid the size of whaleboats were sometimes ejected!

Although regurgitation helped whalemen to identify items in the diet of sperm whales, it may interfere with today's methods of establishing food habits on the basis of stomach contents examined at land stations. Matthews (1938, p. 122) found eleven of seventy-four whales with empty stomachs, but this report may be misleading because the stomach contents may have been ejected at capture. Betesheva and Akimuskin (1955, p. 93) believed that regurgitation may have accounted for some of the empty stomachs they found in their examination of sperm whales caught off the Kurile Islands.

Squid is undoubtedly the most important food item for sperm whales. Although octopus and cuttlefish are often mentioned as part of the diet (Millais, 1906, p. 292; Mizue, 1950, p. 116; Omura, 1950, p. 102; Mizue, 1951, p. 89), seven species of squid formed 80 per cent of the diet of whales from the Kurile Islands area. Octopus constituted less than 4 per cent of the cephalopods (Betesheva and Akimuskin, 1955, p. 93). More than 28,000 squid have been taken from the stomach of one sperm whale (Akimuskin, 1955). Thirty-two squid averaging about 2.2 meters in overall length, each weighing 8.2 kilograms, making 262 kilograms of food, were removed from another whale's stomach (Clarke, 1954*a*, p. 313).

The average size of squid eaten in the antarctic is slightly larger (1.3 meters) than those eaten in the North Atlantic (0.94 meters) (Clarke, 1955, p. 353). Lillie (1955, p. 93) recorded 2.2 meters as the size of the largest squid he saw in stomach contents in the antarctic, but one enormous intact squid was recovered from a 14.6-meter sperm whale captured in the Azores. The latter squid weighed 184 kilograms and measured 10.49 meters in total length (Clarke, 1955, p. 355). In the eastern Pacific, Rice found nineteen large *Moroteuthis robusta*, averaging about 16 kilograms each, in the stomach of a sperm whale, making about 300 kilograms in all.

Scratch marks left by squid are frequently found around the mouths of sperm whales (Pike, 1953, p. 100; Ash, 1962, p. 67, and photograph on p. 62). These marks are 2 to 3 meters in length (Matthews, 1938, p. 122). Sucker marks of squid tentacles also give mute evidence of the struggle that takes place in the ocean depths. Sucker marks, which range up to 10 centimeters in diameter (Matthews, 1938, p. 122), have been illustrated (Hjort, 1933, p. 15). These marks may be in long regular rows (Mielche, 1952, p. 43).

Scars caused by cephalopods are found more frequently on male sperm whales than on females; Matthews (1938, p. 122) therefore reasoned that females do not attack squid so large as those attacked by males. All the big squid that Rice found were in the stomachs of large male whales.

The species of squid encountered are not the common upper-layer forms, but the deeper-dwelling species (Betesheva and Akimuskin, 1955, p. 93; M. R. Clarke, 1962).

After squid, fish is the most frequently cited item of diet. In the Kurile Islands fish were found in 30 per cent of the stomachs examined, but only in small quantities (Betesheva and Akimuskin, 1955, p. 93). In the Azores fish were found in 14 per cent of the stomachs, and, in the antarctic, 13 per cent of the stomachs examined contained fish (Clarke, 1956*c*, p. 259).

The fish found in sperm whale stomachs are usually deepwater species. Sharks have frequently been reported (Bennett, 1840, II, 176; Millais, 1906, pp. 285, 292; Andrews, 1916, p. 230; Mizue, 1951, p. 89; Betesheva and Akimuskin, 1955, p. 93; Clarke, 1956*a*, p. 442; 1956*c*, p. 261). A 10-foot blue shark was recovered from one stomach (Norman and Fraser, 1949, p. 262). Other species reported are rock cod (Bennett, 1840, II, 176; Bullen, 1899, p. 342; Omura, 1950, p. 102), scorpaenids (Mizue, 1951, p. 89), snapper (Bullen, 1899, p. 342), barracuda (Bullen, 1899, p. 342; Clarke, 1956*a*, p. 442; 1956*c*, p. 260), sardines (Mizue, 1951, p. 89, ragfish (Robbins *et al.*, 1937; Pike, 1950), skates (Millais, 1906, p. 292; Pike, 1950), albacore (Clarke, 1956*a*, p. 442; 1956*c*, p. 260), angler fish (Millais, 1906, p. 292; Clarke, 1954*a*, p. 310; 1956*a*, p. 442; Gates, 1958, p. 564), and rattails (Betesheva and Akimuskin, 1955, p. 93). The lampreys that attack sperm whales have also been found in their stomach contents (Robbins *et al.*, 1937; Pike, 1950). Rice (1963) found the deepwater brown cat shark (*Apristurus brunneus*) and many longnose skates (*Raja rhina*) in stomachs of sperm whales taken off San Francisco, California.

An interesting report that has appeared more than once is that fishing tackle has been found in sperm whale stomachs. It has apparently been ingested along with fish stolen from fishermen's lines. Both fishing lines and shell hooks have been recovered (Turner, 1903, p. 424; Millais, 1906, p. 285; Degerbøl, 1940, p. 113).

Seal vibrissae also have been recovered (Murphy, 1924; 1933, p. 125).

The list of invertebrates, in addition to cephalopods, recovered from sperm whale stomachs includes spiny lobsters (Andrews, 1916, p. 230), crayfish (Ash, 1962, p. 67), crabs (Nemoto and Nasu, 1963, p. 83), jellyfish (Mizue, 1950, p. 116; Clarke, 1956*c*, p. 261), sponges (Nemoto and Nasu, 1963, p. 83), and tunicates (Clarke, 1956*c*, p. 261).

Mizue (1951, p. 89) suggested that the diet of the male sperm whale is more varied than that of the female.

Foreign materials are occasionally ingested. Nemoto and Nasu (1963, p. 85) listed stone and rock fragments up to 1.4 kilograms in weight, and sand up to 4 liters in volume (p. 87). Their list of other foreign objects included a glass buoy, a coconut, and the cut meat of a baleen whale (p. 83). Pike (1950) also reported finding a stone, a piece of wood, and an apple. A possible piece of coral has also been reported (Clarke, 1956*c*, p. 261). Rice found a shoe, a plastic bag, baling wire, and gorgonians.

The foreign materials reportedly ingested by sperm whales in the wild are similar to items swallowed by captive cetaceans. One captive Pacific pilot whale (*Globicephala scammoni*) swallowed a 45- by 10-centimeter inflated rubber inner tube (Brown, 1960, p. 345), and other captive pilot whales ingested rock fragments (Brown, 1962, p. 63). During the years 1955 to 1958, most of the mortality in dolphins at Marineland of the Pacific was caused by ingestion of foreign material. One Pacific striped dolphin (*Lagenorhynchus obliquidens*) ingested a 12.5-centimeter piece of wood, a 10-centimeter rubber ball, and a piece of rubber sponge; another of the same species swallowed seven cotton gloves (Brown *et al.*, 1960, p. 534, fig. 1, and p. 537). A Pacific bottlenose dolphin (*Tursiops gilli*) took in, but regurgitated, gravel and rock particles (*ibid.*, p. 536). A young captive *Tursiops truncatus* died from an impaction caused by eating turtle grass (McBride, 1940, p. 29).

From the list of items recovered from their stomachs, it is apparent that sperm whales feed both in mid-water, where they would obtain most of the squid, and on the bottom, where they would obtain most large octopuses, essentially all skates, and, incidentally, the miscellaneous items.

Whalers have long recognized a correlation between the moon phases and the abundance of sperm whales on certain whaling grounds. Holm and Jonsgård (1959), after a statistical analysis of antarctic sperm whale catches, suggested that sperm whales tend to congregate in schools near shallow banks at about the time of the full moon and the new moon. This tendency may possibly be correlated with the behavior of squid, but more research on this subject is needed.

Neither blindness, deformed jaws, nor worn teeth seem to interfere markedly with feeding. Beale (1839, p. 36) reported the capture of a blind sperm whale in excellent condition. Bullen (1899, p. 121) notes that three whales with deformed jaws, all of them low in oil content, were captured, but adds that sperm whales with deformed jaws had been taken which were in excellent condition. Ash (1962, p. 67) reported that none of four sperm whales with injured or deformed jaws was thin. Beale (1839, p. 36) noted that two animals with deformed jaws were in good condition. In old sperm whales, the teeth become worn and rounded (Gray, 1844–1875, p. 21; Davis, 1926, p. 171), and may even be worn to the gum line (Scammon, 1874, p. 18; Gelett, 1917, p. 78; Davis, 1926, p. 186). Although Scammon (*loc. cit.*) said that whales become emaciated when their teeth wear down, it is not likely that the emaciation is a result of the wear on the teeth, but rather that the events are concurrent; sperm whales apparently do not use their teeth as a major mechanism for feeding, but for fighting (see pp. 693–694, above). Rice has examined many large, fresh squid taken from sperm whale stomachs, and only rarely has noted tooth marks on them; usually they are almost completely undamaged. It should be repeated here that the teeth do not even erupt until sexual maturity, at an age approaching nine or ten years. Food may be ingested by a sucking motion of the tongue.

Nothing is known of the sperm whale's method of looking for food. It would seem likely, however, that echolocation is used to locate prey at the depths where sperm whales feed. There is, however, a Russian report (Tarasov, 1960, p. 33) of the capture of a deaf but well-fed sperm whale, suggesting feeding without echolocation. The author did not state how deafness was demonstrated. Heezen (1957), in attempting to explain how sperm whales become entangled in deep-sea submarine cables, suggests that the animals skim along the bottom with the lower jaw in the sediments, searching for food.

Only one man has had the opportunity to see a sperm whale feeding. At 11:00 P.M. one night, by night glass and moonlight, Bullen (1899, p. 143) observed a cephalopod and a sperm whale engaged in a struggle. The whale seemed to have the tail part of the cephalopod in its mouth. Sharks were attracted to the scene, and this attraction may account for the frequency of reports that sharks are found in sperm whale stomach contents.

It has been suggested that the throat grooves prominent in the sperm whale may allow for throat distension and passage of such large food items as the 3-meter shark and the 10.49-meter squid mentioned above (Beddard, 1900; Stead, 1930; Boschma, 1938, p. 157; Clarke, 1956*c*, p. 247).

Thompson (1928, p. 15) stated that the sperm whales captured at Scottish whaling stations in 1911 were fat, whereas those captured in 1909 and 1912 were lean. This disparity suggests a yearly difference in food supply. Clarke (1954*a*, p. 312) believes, however, that sperm whales can find something to eat at any season at any point in their wide geographical range. The variety of their dietary items would tend to support this opinion.

EXCRETION

The aspect of sperm whale digestion which preoccupied most of the earlier observers was the presence of ambergris, the valuable commodity that is occasionally found in the stomachs or the intestines of sperm whales. Ambergris is an abnormal concretion thought to be the result of fecal impaction (Clarke, 1954*c*, p. 289). The substance is produced by both sexes (Murphy, 1933, p. 123). The largest lump of ambergris recorded weighed 455 kilograms, and was recovered from a sperm whale taken off New Zealand (Tønnessen, 1962, p. 477).

Although ambergris is an abnormal product of the digestive tract, the aliphatic alcohol ambrain contained in ambergris seems to be a normal product in sperm whale feces. It has been suggested by Raymond Gilmore (personal communication to Rice) that this aromatic substance may serve a communicatory function via the gustatory senses. In view of the wide use of such olfactory communication in land mammals, and Slijper's (1962, p. 292) description of ambergris as smelling of musk, Gilmore's suggestion warrants attention.

The sperm whale apparently has the usual mammalian reactions to fear and excitement, as it has been reported to defecate under such conditions (Clarke, 1956*b*, p. 315).

SOUND PRODUCTION

The internal anatomy of the sperm whale auditory apparatus has been investigated and shown to be well developed (Yamada, 1953). The acoustic system of the odontocete brain, including that of the sperm whale specifically, has reached a peculiar stage of development which is unique among mammals (Ogawa and Arifuku, 1948, p. 12). For exploration of the environment, this acoustic system may well serve in the stead of primate hands and well-developed stereoscopic vision.

Early whalemen knew from practical experience that sperm whales have an excellent organ for hearing (Beale, 1839, p. 30). They were extremely careful to approach a whale in silence, as any abrupt sound stimulus would put the animal to flight. Clarke (1956*b*, p. 315) states that sperm whales are not affected by the direct hit of a whale mark, but are frightened by the sudden sound of the splash if a mark misses. On the other hand, the sound of an approaching motor, which grows slowly but progressively louder, does not seem to startle sperm whales; there must be an abrupt change in sound stimulus to elicit alarm.

Audible sound production in air must be a rare occurrence, as Beale (1839, p. 3) stated that he had never heard sperm whales make sounds. Several years later, however, Bennett (1840, II, 206) referred to a creaking sound emitted by the sperm whale. The significance of what he heard would not be understood for another century.

Worthington and Schevill (1957) describe three types of underwater sounds produced by a school of sperm whales: a muffled smashing noise, a low-pitched groan or rusty-hinge creaking, and a series of sharp clicks. Haas (1959, p. 185), in making underwater observations, heard the creaking sound, and noted that it could be created with the mouth either open or closed. The clicking sound was heard by Gilmore (1961, p. 96) when live harpooned sperm whales were brought alongside a catcher boat. Later, Schevill and Watkins (1962, phonograph record, side 2, pt. 7) apparently considered the creaking and clicking sounds to be basically the same, as Schevill stated that the clicking sound was the only sound ever heard from sperm whales. A sonagram of the clicks has been illustrated by Schevill *et al.* (1962, p. 557). In her review of marine mammal sounds heard by American submariners in Pacific waters, Fish (1949, p. 55) attributed the many scattered records of marine mammals from the open ocean to sperm whales, as they are known to range these areas at all times.

Sperm whales are reported to communicate alarm almost instantly over distances of up to 6 or 7 miles (Bennett, 1840, II, 178; Hopkins, 1922, p. 61; Davis, 1926, p. 180; Ashley, 1942, p. 80; Gilmore, 1961, p. 96). The sperm whales to which the alarm is communicated may then either flee or come to the assistance of the injured individual.

Tomilin (1955, p. 30) believes that sonic signaling is especially well developed in sperm whales, as they have an extremely complicated nasal structure. Sperm whales are also known to receive high-frequency sounds, for they leave an area where a ship's Fathometer is operating. Whalers switch off their depth-finding apparatus when hunting sperm whales.

SENSES

Hearing

External examination of the sperm whale ear could easily lead to the assumption that this organ is unimportant. The external opening is not more than half a centimeter in diameter (Scammon, 1874, p. 75). The opening is so small as to create doubts that the external hearing is functional, but the most recent investigations (Fraser and Purves, 1960, p. 136) have bolstered the idea that hearing in the Cetacea is "by way of the functional external auditory meatus as in terrestrial mammals."

Gustatory Senses

A true sense of smell of airborne odors, like that of land mammals, probably does not exist in the odontocetes. Toothed whales, after birth, have neither olfactory nerves nor olfactory lobes of the brain (Tomilin, 1955, p. 16), although they are found in the embryos (Kellogg, 1938, p. 666).

Yablokov (1957, 1961) points out, however, the presence of what he terms "olfactory pits" at the root of the tongue. By means of these pits, a waterborne chemical sense is permitted, and could conceivably be carried to the unreduced olfactory region of the cerebral cortex. Yablokov (1961) also notes the presence of a preanal gland in both the male sperm whale and the beluga which opens directly into the water, and frequent urination in cetaceans. Chemical communication may therefore be present in these two species. Lilly (1961, p. 163) suggests the possibility of gustatory communication in *Tursiops truncatus* by means of excreta.

As chemicals in water are dispersed at best at a rate of a few meters per second (Schevill *et al.*, 1962, p. 554), however, a gustatory sense in cetaceans would always play a secondary role to the highly developed auditory sense. A somewhat higher dispersal rate might be expected when chemicals are carried by currents or by a moving animal "laying a trail."

Vision

Although hearing is doubtless the dominant perceptive pathway in the sperm whale, vision above water is reported to be very good (Beale, 1839, pp. 30, 47; Bennett, 1840, II, 180). The anatomy of the sperm whale eye has been discussed by Rochon-Duvigneaud (1940, p. 68). Because of the extreme lateral placement of the eye, however, there is no vision either directly in front of or directly behind the head. This blind sector has been estimated as extending through about 10 degrees in front and 40 to 50 degrees in the rear (Ashley, 1942, p. 78). In order to take advantage of these blind spots, early whalemen approached either directly from the front or rear, keeping spout and hump in a single line of sight (Brown, 1887, p. 263).

Inasmuch as the eye is well developed and immersed most of the time, Kellogg's (1938, p. 662) suggestion that, underwater, all whales are subject to myopia and astigmatism seems highly unlikely.

CONCLUSIONS

In a review paper of this kind, it is difficult to summarize without repeating more of the text than is practical. The table of contents provides a brief summary of the topics covered.

In conclusion, however, we wish to point out that our findings indicate that there is no essential difference between the behavior of sperm whales, except for reasons of special adaptation to the aquatic environment, and the behavior of large terrestrial mammals with similar food requirements and internal social organization.

(After our paper was in the proof stage, we discovered a recent article [Gaskin, 1964] which is closely related to our own presentation. Although short, the article gives important data on various aspects of sperm whale behavior: distribution and sexual segregation, swimming speeds, spouting rhythms, feeding and diving, and reactions to boats and other causes of extraneous sounds.)

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COMMENTS

Dr. Lilly: I had occasion to research the question of the behavior of sperm whales in the early whaling men's logs of their ships. I was specifically interested in the attacks of sperm whales on boats and ships. I looked for unprovoked attacks on boats before a harpoon had been thrown. In four instances which newspapers described as unprovoked attacks, the logs said that an iron had been thrown into the particular animal.

Mr. Wood: Your statement that sperm whales take flight to windward is interesting and puzzling, if indeed they do. It seems to me that you implied this behavior has some survival value.

Dr. Caldwell: No, we were just pointing out that it has been suggested that perhaps the flight to windward is a holdover from some time past, when whales had a sense of smell. We don't have any idea what the reason might be. In fact, one reference states that the animals did not flee to windward, probably because it was so obvious or so interesting to the observer.

Dr. Lilly: Could it be because a square-rigged ship cannot sail to windward?

Mr. Schevill: As for the business of going to windward, I think Dr. Lilly is close to the answer. It is, of course, the irritating behavior that the logkeeper would remember. On the other hand, we also note very often, possibly with the same emphasis, that other cetaceans go to windward. I don't follow the idea of smell. If it is a vestigial olfactory reaction, I would think it would be a wrong one. If the animal went to windward, it would leave a nice trail. If it went to leeward, it would take the trail with it.

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A FURTHER NOTE ON THE CONSTRUCTION OF THE PYRAMIDS. In the January *Geographical Review* Professor Philip Kissam has commented on the theory developed by Mr. Edward J. Kunkel that the great pyramid of Giza (and perhaps other pyramids) was designed and built as a hydraulic structure (Philip Kissam: A New Concept of the Construction of the Pyramids, *Geogr. Rev.*, Vol. 56, 1966, pp. 121–123). It occurs to the present writer, a marine biologist, that Kunkel's hypothesis would be supported if "fossil" remnants of aquatic plants and animals could be found within the pyramids.

The possibility of finding such "fossils" rests on an implication of the Kunkel hypothesis, namely that the pyramid formed an open freshwater pond during much of the period of its construction. This pond would almost certainly have become inhabited by a variety of small aquatic organisms such as algae, protozoans, nematodes, crustaceans, insects, and perhaps snails. Many of these (for instance, diatoms, ostracods, and insects) have siliceous, calcareous, or chitinous "skeletons," which, when their owners die, resist decay and accumulate on the bottom. There they may last indefinitely if protected from chemical action and weathering. Furthermore, such skeletons are often identifiable with precision as to the kinds of organisms of which they were originally a part.

Most of the skeletal remains would be microscopic and therefore not apparent to casual inspection. They would simply be components of the dirt on the horizontal surfaces formerly covered by water. It is especially likely that they would be preserved in grooves or crevices in the horizontal surfaces—for example, in the "notches on the inside of the top of each stone" mentioned in Professor Kissam's note (p. 122).

If places where skeletons of aquatic organisms would have settled out of the water are accessible, then to obtain samples for examination would be easy. Small amounts of the dirt could be picked out of the grooves and crevices, with the use of something like a needle or ice pick, and placed in vials or small bottles, carefully labeled as to location. Samples from about ten different levels of the pyramid would be adequate, at least as a preliminary. The samples would, of course, have to be from places that have been protected from wind and rain since the pyramids were built.—J. Lockwood Chamberlin

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The Texas Basins Project[1]

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ABSTRACT

The Texas Basins project is part of a plan to develop water resources of Texas to meet projected municipal, industrial, and insofar as possible, irrigation requirements in the year 2010. Eighteen reservoirs would supply water to a trans-Texas canal which would intercept tributary discharge to all coastal marshes. The large anticipated demands not related directly to the project, combined with project diversions, would reduce by one-half the average annual freshwater flow of 26½ million acre-feet now reaching Texas estuaries. The reduction could exceed 75 percent during dry years. The Texas Basins project would account for about one-third of this reduction.

About 1⅓ million acres of tidewater in Texas yield about 200 million pounds of fish and shellfish annually to commercial fishermen, and support more than 7 million man-days of sport fishing. Expected expansion of commercial and sport fisheries will be restricted if the amount of fresh water reaching the coast is reduced permanently and significantly. Reduction of tributary discharge attributable to the project, and the introduction of toxic pesticides into two estuaries from adjacent irrigation units, could cause annual losses of an estimated 118 million pounds of commercial fishery products, and nearly 3 million man-days of sport fishing.

Losses could be prevented and certain benefits realized by enlarging the scope of the Texas Basins project to provide for maintenance of estuarine fishery resources, and to prevent the discharge of toxic pesticides.

INTRODUCTION

The proposed Texas Basins project is an integral and significant part of a statewide distribution system that would provide water to meet anticipated municipal and industrial requirements in the year 2010. It would also permit development of more irrigable lands. The overall plan is essentially the one adopted by the U. S. Study Commission for Texas in 1962.

The population of Texas is expected to grow from 9.6 million people in 1960 to nearly 23 million in 2010. Accordingly, municipal and industrial water needs during this period will increase from 1.7 million to over 12 million acre-feet per year. About 105 small and intermediate-size reservoirs supplied water in 1960. It is now estimated that to meet the water demands of 2010 an additional 70 major reservoirs will be required, together with a transport system to deliver the water where and when needed. The Texas Basins project would supply about one-eighth of the projected requirements for municipal and industrial use, plus enough water to develop 785 thousand acres of new irrigated farmland. It would also afford a nominal amount of flood control and provide some recreational benefits. In its development additional consideration would be given other purposes such as navigation, power, improvement of water quality, and fish and wildlife.

Information on municipal, industrial, and agricultural water requirements, and on details of the Texas Basins project was obtained from unpublished reports and records of the U. S. Bureau of Reclamation and the Fish and Wildlife Service, although much of the descriptive material contained herein has been released to various news media in condensed form. An example of many such releases is that by Pyle (1963) who, like others in similar circumstances, gave little attention to the probable effects of such projects upon coastal fish and wildlife resources. In all fairness to such reporters, however, they are usually not made fully aware of what is at stake for these natural resources. Conservationists must therefore improve their channels of communication.

Fortunately, the Congress of the United States has recognized the importance and value of fish and wildlife resources, in addition to the need to plan and coordinate properly all Federal as well as privately sponsored water development projects involving the country's navigable waters. Legislation enacted in 1946 charges the U. S. Fish

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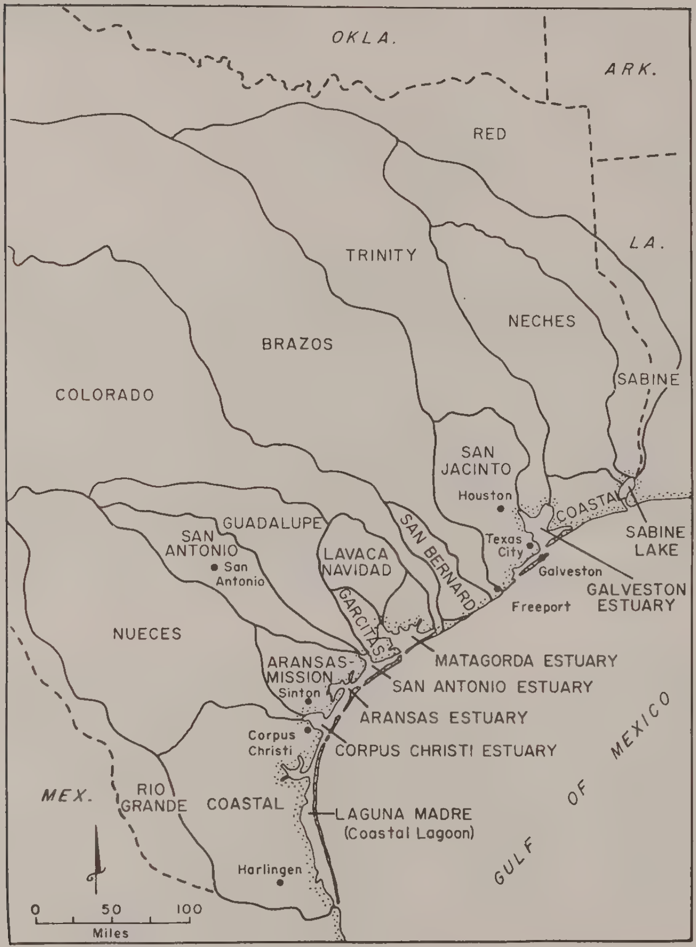
[1] Contribution No. 206, Bureau of Commercial Fisheries Biological Laboratory, Galveston, Tex.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SAN ANTONIO
San Antonio
LAVACA NAVIDAD
SAN BERNARD
Texas City
SABINE LAKE
Galveston
GALVESTON ESTUARY
Freeport
GARCITAS
NUECES
MATAGORDA ESTUARY
ARANSAS-MISSION
Sinton
SAN ANTONIO ESTUARY
ARANSAS ESTUARY
Corpus Christi
CORPUS CHRISTI ESTUARY
GULF OF MEXICO
MEX.
RIO GRANDE
COASTAL
LAGUNA MADRE (Coastal Lagoon)
Harlingen
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Miles

FIGURE 1.—Major river basins and estuaries in Texas.

and Wildlife Service with the responsibility of protecting the public's interest in the fish and wildlife resources so affected. Thus, under authority of the Fish and Wildlife Coordination Act (48 Stat. 401, as amended; 16 U.S.C. 661 *et seq.*) the Service, in cooperation with appropriate state conservation agencies, reviews these projects to evaluate their potential effects and, if necessary, to recommend changes that will benefit or will minimize anticipated damage to these valuable living resources.

The Fish and Wildlife Service has a tremendous task in discharging its responsibility under the Coordination Act. Literally thousands of water development projects are in the planning stage, have been authorized, or are under construction. They vary in scope from small single-purpose efforts such as the construction of wharves or piers, to large navigation channels and multi-purpose projects which involve the water resources of an entire river basin or, in the case of the Texas Basins project, a series of river basins. The potential effects of such an array of diversified activities upon coastal fish and wildlife resources are as varied and complex as the projects themselves (Diener, 1965; Kutkuhn,

TABLE 1.—*Texas estuaries and their major subdivisions*

Estuary	Major components	Tributary rivers	Area in surface acres
Sabine Lake	Sabine Lake	Sabine, Neches	45,000
Galveston	Galveston Bay East Bay Trinity Bay West Bay	Trinity, San Jacinto	336,000
Matagorda	Matagorda Bay Lavaca Bay	Lavaca (with Navidad)	233,000
San Antonio	San Antonio Bay Espiritu Santo Bay Mesquite Bay	Guadalupe (with San Antonio)	138,000
Aransas	Aransas Bay Copano Bay Redfish Bay Mission Bay	Mission, Aransas	127,000
Corpus Christi	Corpus Christi Bay Nueces Bay	Nueces	116,000
Laguna Madre[1]	Upper Laguna Baffin Bay Lower Laguna	—	317,000
TOTAL			1,312,000

[1] Hypersaline coastal lagoon; not a true estuary.

Source: Navigation charts prepared by the U. S. Coast and Geodetic Survey.

1965). The one project, however, which promises to affect most adversely the fish and wildlife resources in the Gulf Coast area is the Texas Basins project. The Fish and Wildlife Service therefore has assessed its probable effects and attempted to find solutions to the problems it poses (U. S. Fish and Wildlife Service, 1963, 1964a, 1965).

All tributary discharge and return-flow data employed herein were obtained from records of the U. S. Bureau of Reclamation (unpublished). Fishery statistics were extracted from U. S. Fish and Wildlife Service publications as follows: "Fishery Statistics of the United States" (by years, 1950–61); "Gulf Coast Shrimp Catch by Area and Depth" (by months, January 1956–December 1962); "Texas Landings" (by months, January 1950–December 1962); and "Shrimp Landings" (by months, January 1956–December 1962).

DESCRIPTION OF THE PROJECT

Area of Influence

The structural features of the Texas Basins project would be located in the Gulf Coast region of Texas and in the inland portions of the Sabine, Neches, Colorado, Guadalupe, San Antonio, and Neuces River Basins (Figure 1). The area influenced by the project would include about two-thirds of the state, and particularly its major coastal bays and lagoons. From east to west these coastal waters are Sabine Lake, the Galveston, Matagorda, San Antonio, Aransas, and Corpus Christi estuarine systems, and the hypersaline Laguna Madre (Figure 1). The combined areas of the estuaries and coastal lagoons exceed 1.3 million surface acres (Table 1).

Plan of Development

Project features are divided into two groups. Group I includes the interbasin canal, seven major reservoirs, three reregulating reservoirs (for irrigation), and three irrigation units containing 750 thousand acres. Group II features include 11 major reservoirs and 3 smaller irrigation units totaling 35 thousand acres. Group I facilities would be supplemented by five nonproject reservoirs (Figure 2).

The key element of the proposed Texas Basins project is the interbasin canal which would be a man-made river paralleling the Gulf Coast for 418 miles from the Sabine River to the lower Rio Grande Valley. Its capacity would vary between 2,000 and 5,900 cfs. Structures on the canal would include nine large pumping plants and nine large siphons at stream crossings. Three project reservoirs: Confluence, Sabine Diversion, and Voth; and two nonproject reservoirs, Wallisville and Palmetto Bend, would facilitate transection of major streams. The other Group I reservoirs, Goliad, Liberty, Ponta, and Teneha, would be located inland from, but provide waters for diversion by, the interbasin canal. The Group I irrigation units—Sinton, Baffin Bay, and Lower Rio Grande Valley—would be situated near the cities of Sinton, Corpus Christi, and Harlingen, respectively. A reregulating reservior is planned for each of the three units.

Stages of Construction

Construction of the Texas Basins project would take several decades. Group I facilities would be erected first in several stages. The interbasin canal and the Confluence, Sabine

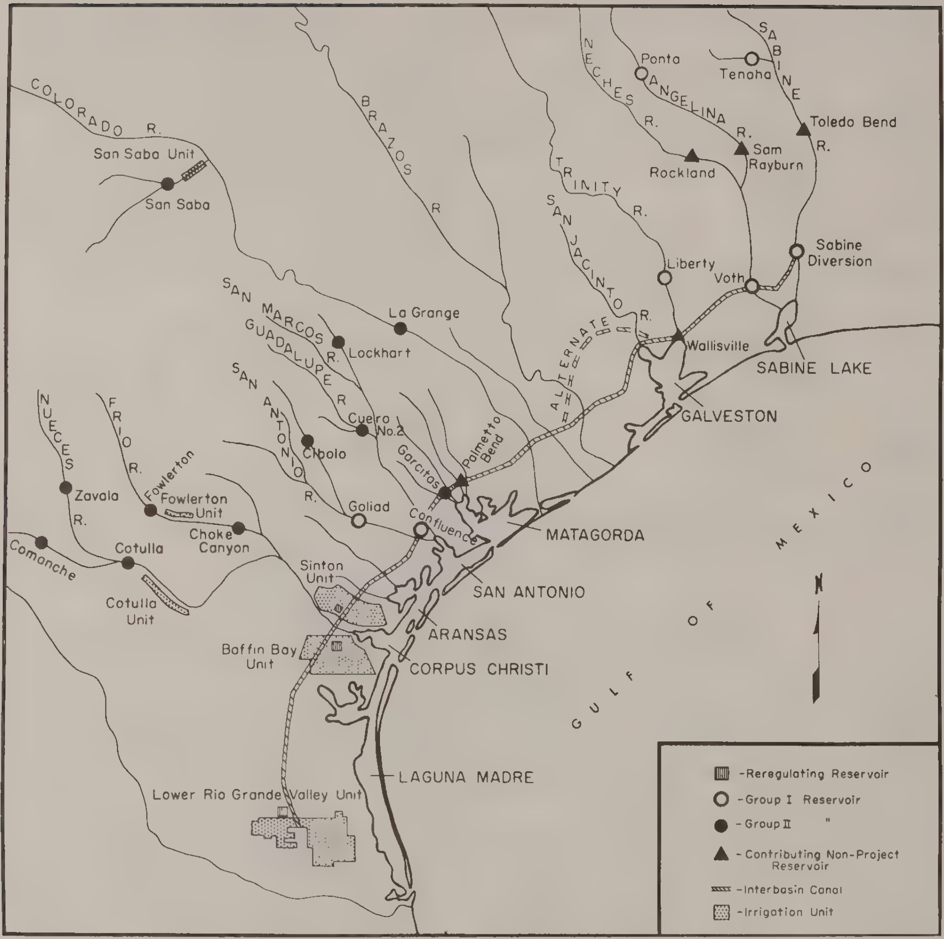
COLORADO R.
San Saba Unit
San Saba
BRAZOS R
NECHES R.
Ponta
ANGELINA R.
Tenaha
SABINE R.
Toledo Bend
Sam Rayburn
Rockland
TRINITY R.
SAN JACINTO R.
Liberty
Voth
Sabine Diversion
Wallisville
SABINE LAKE
ALTERNATE
GALVESTON
La Grange
SAN MARCOS R.
GUADALUPE R
Lockhart
SAN ANTONIO R.
Cuero No.2
Cibolo
NUECES R.
FRIO R.
Fowlerton
Fowlerton Unit
Zavala
Choke Canyon
Cotulla
Comanche
Cotulla Unit
Goliad
Confluence
Garcitas
Palmetto Bend
MATAGORDA
Sinton Unit
SAN ANTONIO
ARANSAS
Baffin Bay Unit
CORPUS CHRISTI
GULF OF MEXICO
N
LAGUNA MADRE
Lower Rio Grande Valley Unit
-Reregulating Reservoir
-Group I Reservoir
-Group II "
-Contributing Non-Project Reservoir
-Interbasin Canal
-Irrigation Unit

FIGURE 2.—Features of the Texas Basins project.

Diversion, Voth, and Valley reregulating reservoirs are included in the first stage, whose completion would require about 10 years. Irrigation, distribution, and drainage facilities are to be built during the second stage. Construction would extend over a 10-year period (after completion of the interbasin canal) for the Lower Rio Grande Valley unit, and 20 years for the Baffin Bay and Sinton units.

During the early years of project operation the supply of water available to the interbasin canal from unregulated stream flow and non-project reservoirs is expected to exceed requirements. Consequently, construction of the Baffin Bay and Sinton reregulating reservoirs, and the Goliad, Liberty, Ponta, and Teneha reservoirs, could be deferred for a number of years until needed to meet increasing demands. Even though construction of Group I facilities would be accomplished in several stages over an extended period, it is likely that authorization for all will be sought in the same legislation.

Demands from the interbasin canal and the development of irrigation units are expected eventually to utilize all Group I water supplies. Thereafter, Group II reservoirs would be

TABLE 2.—*Estimated schedule of development for major features of the Texas Basins project*

Project and supplemental features	Number	Construction schedule or status
Project—Group I		
Interbasin canal	1	10 years
Major reservoirs	7	Within 10–30 years
Reregulating reservoirs	3	Within 10–30 years
Irrigation units	3	Within 10–30 years
Project—Group II		
Major reservoirs	11	As required but probably after 30 years
Irrigation units	3	Not until reservoirs constructed
Nonproject—Supplemental		
Major reservoirs	5	Underway, authorized, or being recommended

Source: Unpublished reports of the U. S. Bureau of Reclamation and Fish and Wildlife Service.

constructed to meet increasing requirements. Authorization for construction of Group II reservoirs will probably be sought individually as the need arises. Table 2 summarizes the estimated construction schedules for major components of the two groups.

Operation

The interbasin canal would intercept and divert stream flow that would otherwise enter Texas estuaries. It would deliver water to communities and cities along the entire Texas coast and supply water to the newly created irrigation units. To accomplish this, the canal would connect basins of major Texas rivers and create a single water supply system for the entire project area.

Tributary Discharge

Historically (1941-57), Texas estuaries have collectively received an average of 26½ million (range 6 to 52) acre-feet of fresh water per year from upland sources.[2] One should readily appreciate that this water is not distributed equally among the various estuaries, the State's easternmost bays and marshes receiving much greater amounts than those in the semiarid southwest. The decline in tributary discharge from east to west is evident not only for average runoff conditions but for years of high and low discharge as well.

The U. S. Bureau of Reclamation has estimated that 52 planned, nonproject reservoirs would reduce average tributary flow entering the estuaries to 18 million acre-feet per year. Project diversions would further decrease the flow so that on the average only 14 million acre-feet would be received annually. During very dry years total discharge (not including return flows) would probably not exceed 1½ million acre-feet, a level so low that it could be expected to have serious consequences. In view of the amount of tributary water received historically by each of the estuaries, the greatest losses based on percentage reduction would occur in the State's central and westernmost estuaries where supplies are even now frequently deficient. Estimated changes from the historic tributary discharge into each estuary are shown in Figure 3.

Return Flows

As tributary discharge to the estuaries declines, return flows, i.e., water diverted from the tributaries, used, and returned as sewage or industrial and agricultural waste, would increase. Thus, in future dry years slightly over one-half (2⅓ of 4 million acre-feet) of the tributary water destined for Texas estuaries is expected to be in this form. We can only speculate as to its probable quality. Hopefully, improved treatment measures and enforcement of pollution-control legislation will permit at least some of the return flow to substitute for unused tributary discharge.

FISHERY RESOURCES

A significant portion of the United States commercial fishing industry is located in the Gulf of Mexico region. From 1950 to 1963, the relative contribution of Gulf landings to the total United States commercial fishery harvest rose from 12 to 29 percent (U. S. Fish and Wildlife Service, 1964a). It follows that the commercial fishing industry of Texas is likewise growing (Figure 4). In recent years, the value of its annual production, which now averages about 200 million pounds of fish and shellfish, has usually exceeded that of other Gulf Coast states, mainly because of large harvests of the valuable brown shrimp, *Penaeus aztecus*.

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[2] Excludes the Colorado River which formerly emptied entirely into Matagorda estuary but now discharges an undetermined amount of water directly into the Gulf of Mexico.

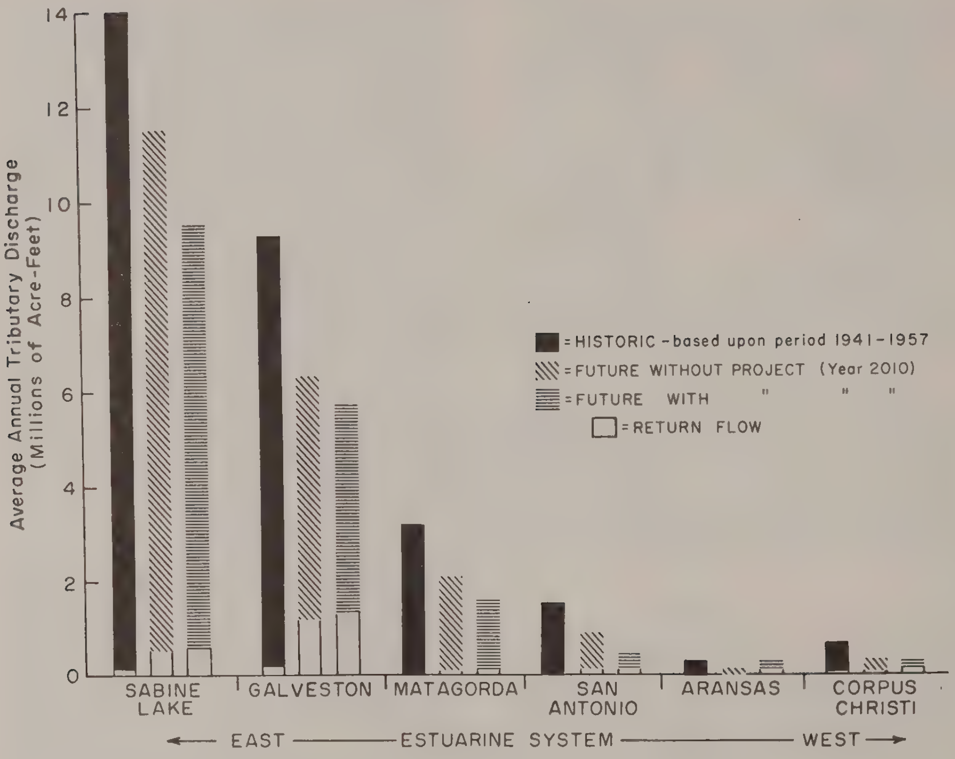

FIGURE 3.—Estimated future change in tributary contributions to Texas estuaries.

Significantly, about 98 percent (by weight) of Texas landings consists of estuary-dependent species (U. S. Fish and Wildlife Service, 1964b). These include both resident and semicatadromous forms. Resident forms are exemplified by the oyster, *Crassostrea virginica*, which completes its life cycle entirely within the estuary. Semicatadromous species include the brown shrimp, *Penaeus aztecus*; white shrimp, *P. setiferus*; largescale menhaden, *Brevoortia patronus*; Atlantic croaker, *Micropogon undulatus*; striped mullet, *Mugil cephalus*; spot, *Leiostomus xanthurus*; sand seatrout, *Cynoscion arenarius*; and red drum, *Sciaenops ocellata*. These species spawn in the Gulf of Mexico, but the young move into the estuary where they grow rapidly to subadults before returning to the Gulf where their life cycle is completed. Other important estuarine-marine species include the blue crab, *Callinectes sapidus*, and the spotted seatrout, *Cynoscion nebulosus*, both of which normally spend most of their lives within the estuary. Fairly large stocks of all of the aforementioned species now exist, but, with the possible exception of the oyster and brown and white shrimps, have been only partially exploited. If suitable environmental conditions in the estuary can be maintained, it is not unreasonable to expect that their overall harvest will more than double over the next three or four decades.

In addition, the U. S. Fish and Wildlife Service (unpublished) has estimated that Texas estuaries annually support more than 7 million man-days of sport fishing for estuary-dependent species. Recreational fishing is also expected to increase significantly as the human population expands. By 2010 the estuaries may be called upon to provide about 17 million man-days of angling.

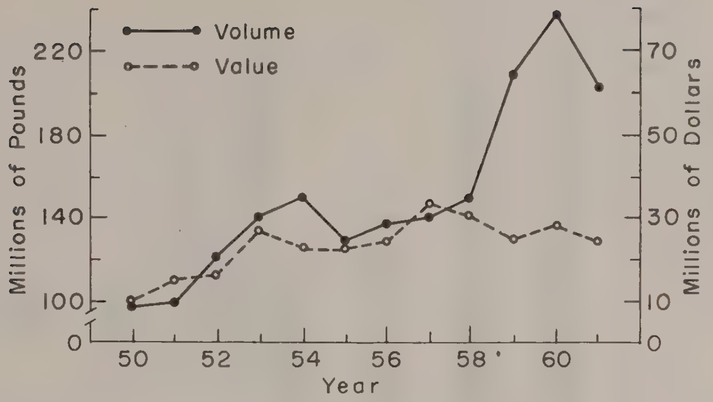

FIGURE 4.—Commercial fishery landings in Texas, 1950–1961.

TRIBUTARY DISCHARGE AND FISHERY HARVEST

Since about 90 percent of the harvest of estuary-dependent fishery resources from Texas coastal waters occurs in the Gulf of Mexico after the various species leave the estuaries, catch statistics alone do not directly indicate the relative importance of individual bay systems in maintaining such resources. It was necessary therefore to develop some means of relating harvests in the Gulf to the particular estuary in which the young of the species involved (chiefly menhaden, and white and brown shrimp) were most likely nutured. Particularly useful in this regard were the facts that harvest areas in the Gulf are accurately known, that white and brown shrimp tend to move southwestwardly along the coast after leaving the estuaries, and that the relative abundance of juvenile shrimp in each estuary has been assessed regularly since 1960 by the Texas Parks and Wildlife Department (unpublished). To apportion the Gulf catch on the basis of estuarine origin, it was therefore assumed that individual bay systems contributed white and brown shrimp to harvests from the adjacent Gulf, and from those waters immediately to the west, in direct proportion to the size of the juvenile populations they harbored. It was also assumed that since menhaden are now taken solely off eastern Texas, only those utilizing the State's easternmost estuaries contribute to Texas landings of this species.

Estuaries in eastern Texas, which receive the greatest amount of tributary discharge in relation to their volume, are believed to contribute more to the well-being of fishery resources harvested commercially in Texas waters than do those lying to the west. As an example, the Galveston estuary, with a high discharge-volume ratio, yields on the average (by weight) about 30 times more commercial fishery products per unit area than does Laguna Madre, which has approximately the same surface area. Generally, the discharge-volume ratio is highest for the easternmost estuaries, declines appreciably in the central estuaries, and reaches its lowest level in the extreme southwest. Harvests of their fishery resources follow a similar pattern although wide variation is evident between individual estuaries (Figure 5).

It is also apparent that the influence of tributary inflow upon estuarine fishery resources varies considerably between estuaries because of differences in basin size and configuration, and in the quantity and quality of fresh water received. For example, the Aransas estuarine system receives less runoff than the San Antonio estuary but yields a greater harvest. Both Copano and Mission bays, in Aransas estuary, are shallow and restricted at their lower ends so that small amounts of tributary runoff measurably affect their suitability as (estuarine) habitat for many species over relatively long periods. Espiritu Santo

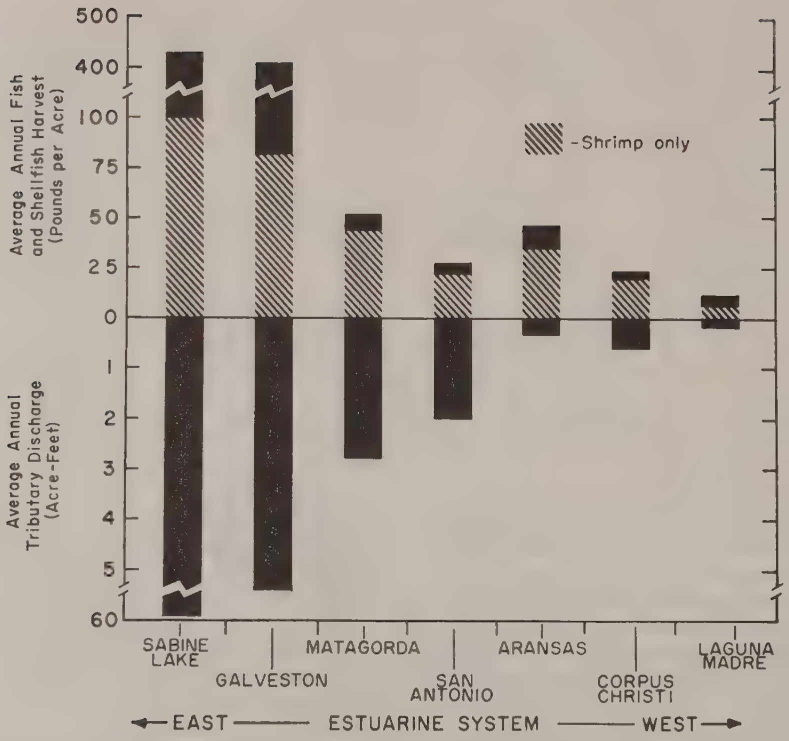

FIGURE 5.—Commercial fishery harvest in relation to amount of fresh water received by Texas estuaries. Tributary discharge has been adjusted for volume of estuarine basin by dividing basin volume by discharge volume. (Period of analysis: 1956–62.)

Bay of the San Antonio estuary, on the other hand, does not receive tributary fresh water directly and its waters are therefore almost as saline as the nearby Gulf. Also, the salinity of San Antonio Bay proper is subject to extreme and rapid fluctuation because of the peculiar pattern of tributary discharge. Thus, each estuary has many unique characteristics that must be considered when assessing the freshwater requirements of the fishery resources inhabiting it.

Even though the trend in commercial fishery production has been upward in recent years, considerable variation in harvest is evident from year to year and between so-called wet and dry cycles. Fishery harvests during a series of wet years are generally greater than those realized in dry years (Figure 6). Excessive tributary discharge into a specific estuary, however, can probably be detrimental if the resulting "freshwater" conditions prevail for long periods. Use of the estuary would then be temporarily restricted to freshwater forms or to those estuary-dependent animals such as the white shrimp or blue crab which can apparently withstand such conditions.

Greatly diminished brackishness often characterizes Sabine Lake in the eastern part of the State but rarely occurs in the central and westernmost estuaries. Conversely, projected reduction in tributary discharge could, in effect, permanently duplicate adverse hydrological conditions that accompany temporary but severe droughts. Thus, abnormally high salinity could be expected in all estuaries except Sabine Lake. Even hypersalinity, as now typifies Laguna Madre, might be expected periodically in those estuaries located along the central and western portions of the coast.

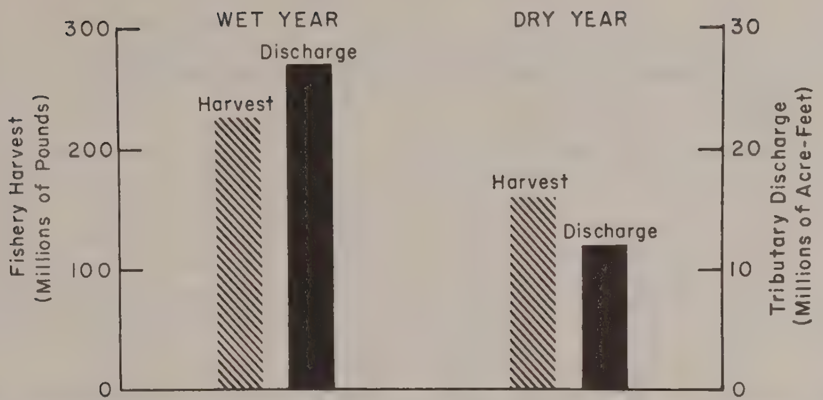

FIGURE 6.—Commercial harvest of estuary-dependent fishery resources from Texas waters during wet and dry years. (Period of analysis: 1956–62.)

Lower yields of fishery resources, which are believed to often reflect such adverse conditions, would then result. However, since losses of tributary discharge would occur slowly as the project develops over a long period the commercial fisheries involved could be expected to continue expanding for many years but thereafter steadily decline.

Since both project and nonproject structures would gradually and permanently lessen tributary discharge into Texas estuaries (Figure 3), we have assumed for purposes of preliminary evaluation that the subsequent effect upon estuarine fishery resources would be in direct proportion to the amount of water diverted. Even if the Texas Basins project should never be built, significant reductions in tributary discharge due to other diversion projects would still appreciably curtail the potential of both commercial and sport fisheries. So the combined effects of all nonproject diversions were determined first to provide a basis ("future without-the-project") upon which the added effects of the Texas Basins project could be evaluated.

Prediction of future fishery harvests with and without the project were based on historic harvest records of fish and shellfish utilizing each estuary for a year during which tributary discharge was at a level comparable to the average discharge expected in the future. Since future flows will decline, the records used to estimate future harvests invariably were those associated with periods of drought. Historically, droughts were relatively short in contrast to the severe, semipermanent drought-like conditions expected in the future. Nontheless, historic records offer the best basis at this time from which to prejudge the effects of depleted tributary flows into the estuaries.

We have estimated that in the 100-year period over which economics of the State's water-resource development program without the Texas Basins project have been analyzed (about 1966–2065), commercial fishery harvests would average about 330 million pounds a year, roughly 150 million pounds below their potential. Under similar conditions the estuaries would support an estimated 14 million man-days of sport fishing, a loss of 3 million.

Tributary discharge would be reduced still more by project diversions. Furthermore, the project would also contribute in return flows to Aransas and Corpus Christi estuaries from adjacent irrigation units, large amounts of toxic pesticides and herbicides, which are known to be harmful to fishery resources (Butler and Springer, 1963). Severe pesticide contamination could virtually eliminate the commercial fishery resources that utilize these bay systems. We have estimated that reduction of tributary discharge attributable to the project, together with the introduction of toxic pesticides, could therefore inflict average losses over the 100-year period of analysis of about 118 million pounds annually to the commercial fishery harvest, and nearly 3 million man-days of estuarine sport fishing.

NEED FOR FURTHER RESEARCH

Combined project and nonproject losses to estuarine fishery resources could be catastrophic to the future of the commercial fishing industry of Texas.

It must be realized, however, that the projections given here are subject to modification. Changes in tributary discharge are predicted upon large increases in population together with attendant industrial and agricultural expansion. Similarly, our estimates of the effects of future changes in tributary discharge upon commercial fishery harvest are based on short-term records. Considerably more research and study will be required before we can predict with reasonable confidence the specific effects of such changes. Even with the limited data available, however, it is obvious that estuarine fishery resources in Texas will face a major problem.

In recognizing the problem and attempting to do something about it, the first big step has been taken toward a solution. Because we acknowledge that the data and information available to us have severe limitations, we have recommended that additional study, as a project responsibility, be undertaken in each of the Texas estuaries to supplement and complement existing research programs. Already, the construction agency is re-evaluating fish and wildlife requirements for the purpose of determining if more project water can be supplied from the larger tributaries so as not to divert excessive amounts from the State's central and westernmost estuaries. Also being considered is the feasibility of developing additional supplies for the estuaries to replace nonproject diversions. And. with proper planning, we further anticipate that the adverse effects often associated with the introduction of toxic pesticides can be completely eliminated.

It is noteworthy, too, that a considerable quantity of water will be developed by the project but not needed until full operation is achieved. Additional supplies could also be developed by advancing the schedule for reservoir construction. Perhaps such "surplus supplies" can be made available to the estuaries to maintain their normal salt balance. Consequently, if the Texas Basins project is expanded to include fish and wildlife resource development as a project purpose, it is entirely possible that freshwater requirements for estuarine fishery resources in Texas can be met for many decades to come.

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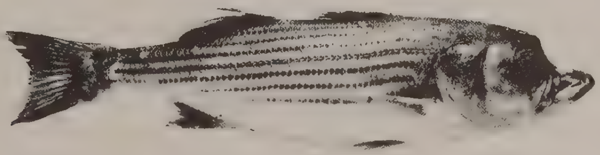
WILDLIFE IN NORTH CAROLINA

June 1966, p. 27

Pugheaded Striper



A pugheaded striped bass, *Roccus saxatilis* (Walbaum), weighing 3 pounds and measuring 19.6 inches fork length, was taken by Sherwood Etheridge in the Roanoke River, N. C., on May 15, 1960. The fish was caught on "cut bait" in the rapids above Weldon, N. C. The specimen, a 4-year-old male, had all the features typical of this abnormality (see photo). It was above the average size (18.3 inches fork length) of normal striped bass of comparable age and was apparently well nourished.

Pugheadedness is thought to result from a germ-cell defect in the embryo, although environmental factors may also contribute. It occurs in several fish species, including brown trout (*Salmo trutta*), carp (*Cyprinus carpio*), white perch (*Roccus americanus*), largemouth bass (*Micropterus salmoides*), and yellow perch (*Perca flavescens*). I collected a pugheaded young-of-the-year American shad, *Alosa sapidissima,* about 4 inches fork length, in the Cape Fear River, N. C., in October 1963.

Pugheadedness is not a rare deformity in striped bass, although to our knowledge none has been previously reported from North Carolina. The specimen from the Roanoke River is in the fish collections of the Zoology Department, North Carolina State University at Raleigh, Raleigh, N. C.

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PROCEEDINGS
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BIOLOGICAL SOCIETY OF WASHINGTON

A NEW TRIBE AND A NEW SPECIES OF OPHIDIOID FISH

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Among the shallow-water, viviparous ophidioids with a separate caudal fin and a hard copulatory apparatus, is a group of several genera which are more closely related to each other than to the *Dinematichthys-Ogilbia* group with which some of them have been confused. Even though much is yet unknown about the species and genera, at this stage in our knowledge of these fishes it seems more desirable to emphasize phyletic *differences* rather than *similarities*. Therefore I propose to segregate these forms into a tribe which is diagnosed below.

I am indebted to the following individuals who have assisted me by commenting on parts of the manuscript. Dr. Bruce Collette, Mr. Charles Dawson, Dr. William Gosline, Mr. R. J. McKay, Dr. Victor Springer, and Dr. Boyd Walker. Curators who have helped me by lending specimens are: Dr. James Böhlke, Academy of Natural Sciences of Philadelphia (ANSP); Mr. R. J. McKay, Western Australian Museum (WAM); Prof. J. L. B. Smith, Rhodes University (RU); and Dr. Frank Talbot, South African Museum (SAM) and Australian Museum (AM). Dr. Talbot has been particularly patient with me, in Cape Town and Sydney, and it is a pleasure to name for him the new species described in this paper.

Definitions of terms and abbreviations are given in Cohen (1964).

DERMATOPSINI, new tribe

Type-genus *Dermatopsis* Ogilby, 1896

Diagnosis: Small, secretive, viviparous ophidioids with a single pair of hard genital claspers (Figs. 2, 4, 5); scales nonimbricate or at most barely overlapping; scales probably lacking on head, but if present, only as a few scattered scales, not as a discrete patch; posterior end of maxillary not greatly expanded vertically (Fig. 1A).

Relationships: Dermatopsini is most closely related to the *Dine-*

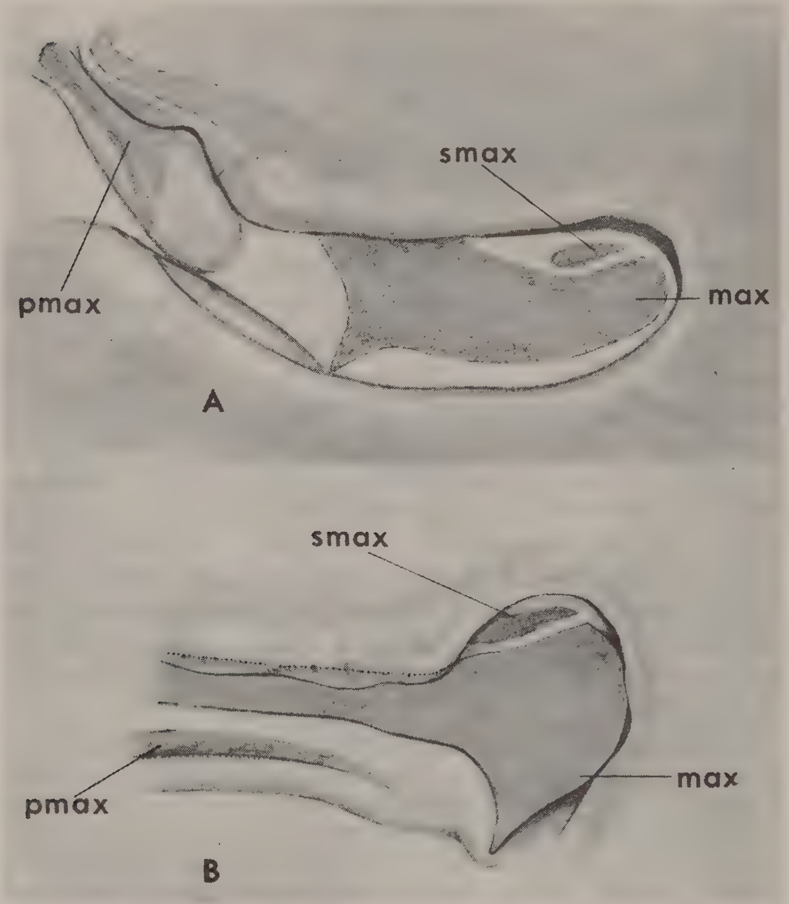


FIG. 1. Alizarin preparations of maxillary bones. Max, maxillary; pmax, premaxillary; smax, supramaxillary. *A.* Horizontally elongated maxillary of *Dermatopsis macrodon,* ANSP-WAS-NZ-1 (see text for data). *B.* Vertically expanded maxillary of *Ogilbia* sp. from USNM 199541, *Te Vega* stat. 106, Indonesia, Mentawei Islands, Pulo Mega; lat. 04°01′S, long. 101°01′30″E. Drawn by Mildred H. Carrington.

matichthys-Ogilbia group, which differs in having multiple pairs of claspers (Turner, 1946), imbricate scales on the body, patches of scales on the head, and the posterior end of the maxillary vertically expanded (Fig. 1B).

Unsolved nomenclatural and zoological problems preclude the presentation of additional discussion or a more formal designation for the *Dinematichthys-Ogilbia* group.

Genera: In addition to the type-genus, I refer to this tribe *Dermatopsoides* Smith, 1947; an as yet undescribed genus from the Gulf of Mexico (Dawson MS); and possibly *Diancistrus* Ogilby, 1898.

Discussion: Four species of small, viviparous ophidioids from the Australia-New Zealand region require comment.

1. *Dinematichthys consobrinus* Hutton, 1875 was described from New Zealand and later figured by Hector (1877). Ogilby (1897) suggested that it might be a species of *Dermatopsis*. The figure shows a relatively short-bodied fish with imbricate scales and the posterior end of the maxillary bone vertically expanded. This species is probably a member of the *Dinematichthys-Ogilbia* group.

2. *Monothrix polylepis* Ogilby, 1897 (monotypic genus) was described from New South Wales and later figured by Whitley (1935). Ogilby suggested relationship with *Dinematichthys piger* Alcock, which he did not think belonged in *Dinematichthys*. The numerous imbricate scales and the shape of the maxillary exclude *M. polylepis* from the Dermatopsini.

Schultz (1960, p. 385) placed *Dermatopsis kasougae* Smith (type-species of *Dermatopsoides*) in the genus *Monothrix*. This would make *Dermatopsoides* a junior synonym of *Monothrix*. On p. 388 of the same paper he listed *Dermatopsoides* as a synonym of *Dinematichthys*. As I show in this paper, these allocations are untenable.

3. *Diancistrus longifilis* Ogilby, 1898 (monotypic genus) was described from Lord Howe Island. I have found no figure or other account of this species in the literature. Schultz (1960) placed *Diancistrus* in the synonymy of *Dinematichthys* with no comment. I believe *Diancistrus* is a valid genus and I tentatively refer it to the Dermatopsini based on the following characters (from the description) in which it resembles several dermatopsine species: head naked, maxillary spatulate, gill membranes united in front, a pair of curved claspers, anal fin united by a membrane to the base of the caudal fin.

4. *Dipulus caecus* Waite, 1905 (monotypic genus) was described and figured from off Fremantle. Waite suggested relationships with the deep sea viviparous ophidioid genera *Aphyonus* Günther and *Sciadonus* Garman. Mees (1962) re-examined the holotype and considered it to represent a species of *Dermatopsis* closely related to *D. multiradiatus* McCulloch and Waite, thus relegating *Dipulus* to the synonymy of *Dermatopsis*. Mees identified a series of specimens from near Perth (Rottnest Island) as *Dermatopsis caecus* (Waite). I quote (p. 28), "The type specimen of *Dipulus caecus* is in the collection of the Western Australian Museum, and although it is in poor condition there can be no doubt about its identity with the fresh material."

I have examined some of Mees' material, and I find it to include three species of ophidioids: a species of *Dinematichthys* (Mees, 1960, reported *D. iluocoeteoides* Bleeker from Rottnest Island); *Dermatopsis multiradiatus;* and *Dipulus caecus.* Mees has confused *D. multiradiatus* and *D. caecus;* my examination of his material shows that these two species differ in many characters. Fin ray and vertebral counts on four specimens of *D. caecus* show 173 to 183 dorsal fin rays, 112 to 120 anal fin rays, and 81 to 86 vertebrae (compared with 98 to 114 dorsal, 64 to 72 anal, and 51 to 55 vertebrae in *D. multiradiatus;* see tables 2, 3, and 5 for frequency distributions). *Dipulus caecus* also has a more elongate body with depth at vent 7.2 to 7.6 percent SL (8.8 to 11.7 percent in *D. multiradiatus*); and a proportionately shorter head, 11.5 to 13.1 percent SL (15.9 to 20.2 percent in *D. multiradiatus*). Other differences are: scales absent in *D. caecus,* present in *D. multiradiatus;* claspers broad, complex, and convoluted in *D. caecus,* not as in *D. multiradiatus* (Fig. 4 B). The two species show many other differences in proportions and in the number and position of head pores.

Several items in the original description of *D. caecus* require discussion. Waite described and figured the dorsal and anal fins as continuous with the pointed caudal fin. R. J. McKay of the Western Australian Museum examined the holotype at my request, and he has written to me that, "The holotype has the caudal fin badly damaged but apparently the dorsal and anal fins were joined to the caudal fin *at the base* of the caudal fin only." This agrees with the tail fins of the specimens which I identify as *D. caecus.* Mr. McKay further wrote ". . . I am unable to ascertain whether the caudal fin of the type was as pointed as Waite illustrates." The caudal fin is rounded in my specimens. The original description of *D. caecus* states that external eyes are lacking in the holotype, a circumstance which McKay has confirmed. The specimens that I have examined all have small but conspicuous eyes, and it therefore seems likely that the holotype is aberrant in this respect. Based on the literature, Thines (1955) included *D. caecus* in a list of blind fishes. In a later paper (1960), however, he examined specimens identified as *D. caecus* and noted the existence of small, but well developed eyes. He gave no information on how his specimens were identified and his observations could have been made on *Dermatopsis multiradiatus* rather than on *Dipulus caecus.*

I recognize *Dipulus* as a valid genus. A proper assessment of its relationships requires further study, and for the present I must relegate it to ophidioid limbo.

Genus *Dermatopsis*

Dermatopsis Ogilby, 1896, p. 138 (type-species by monotypy, *Dermatopsis macrodon* Ogilby, 1896).

Diagnosis: Chin barbel absent. Gill membranes broadly joined to isthmus. Livebearing; male genitalia consisting of fleshy hood, two flattened claspers directed laterally at their distal ends, and penis. Ventral fins immediately adjacent to each other, each with single ray, fins not originating immediately behind symphysis of cleithra, but placed about an interorbital distance behind. Caudal fin free, with 16 or more rays; pectoral fin entire, without separate, elongated rays. Scales lacking on

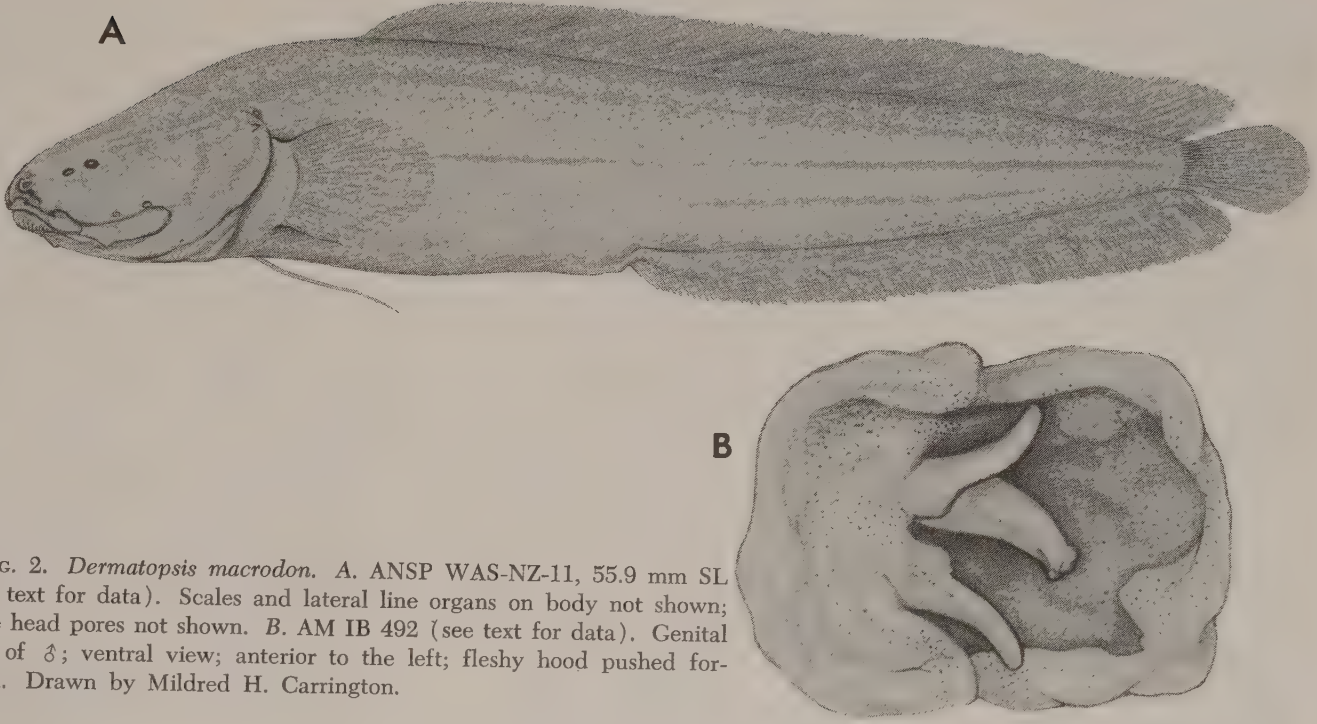


Fig. 2. *Dermatopsis macrodon*. *A*. ANSP WAS-NZ-11, 55.9 mm SL (see text for data). Scales and lateral line organs on body not shown; some head pores not shown. *B*. AM IB 492 (see text for data). Genital area of ♂; ventral view; anterior to the left; fleshy hood pushed forward. Drawn by Mildred H. Carrington.

head, non-imbricate on body. A short, sharp spine at upper angle of opercle. Anterior nostril tubular, located directly above upper lip; gill rakers reduced. Branchiostegal rays 6. Lateral line of minute delicate papillae (not visible in most specimens). Teeth present on premaxillary, vomer, palatine, and dentary; maxillary elongated posteriorly but not vertically expanded. Eyes small. Peritoneum pale.

First neural spine shortest; neural spines on abdominal centra with sharp tips. Vertebrae 1 through 5 or 6 with ribs articulating with centra; parapophyses beginning on centrum 6 or 7.

Description: In addition to the diagnostic characters given above, the following characters are common to the known species and are not repeated in the species accounts. Rounded caudal fin free from dorsal and anal fins in most specimens; however, in a few the fins are joined at their bases. Rays of ventral fins thick proximally but tapering to filamentous tips which do not extend beyond level of posterior end of pectoral fin. Pectoral fin broad and fanlike and inserted vertically on a broad muscle pad.

Head posterior to eyes compressed. Snout slightly depressed. Posterior nostril in front of eye with raised, fleshy rim. Short, tubular anterior nostril at anterolateral corner of snout immediately above lip.

Species: I recognize two. *D. macrodon* has been known heretofore only from New South Wales. I have examined material from North Island, New Zealand as well. The two populations show some differences, and may prove taxonomically separable. *D. multiradiatus* has been known heretofore from Kangaroo Island and the Great Australian Bight. The specimens from near Perth identified by Mees (1960) as *Dermatopsis caecus* (Waite) are both *D. caecus* and *D. multiradiatus*. The Western Australian and South Australian populations of *D. multiradiatus* may be separable.

Dermatopsis macrodon Ogilby

Figs. 1A, 2A, 2B, 3

Dermatopsis macrodon Ogilby, 1896, p. 140 (orig. descr., Maroubra, New S. Wales, near Sydney).—Ogilby, 1897, p. 86 (descr., Maroubra).—Whitley, 1935, p. 239, Fig. 8 (descr., refs., 20 spec. in Australian Museum from vicinity of Sydney).—Thines, 1955, p. 42, 78 (brief descr., listed as blind).

Diagnosis: A *Dermatopsis* with 71 to 80 dorsal rays, 45 to 57 anal rays, 39 to 45 vertebrae, and depth at vent 4.5 to 6.9 in standard length.

Study material: AUSTRALIA, NEW SOUTH WALES, all from near Sydney: AM I.12658, 1 specimen, Maroubra; AM IA.697, 2, Cogee; AM IB.512, 1, Sandor River (under rock); AM IB.7338, 3, inside North Head near Quarantine Beach, Manley; AM IB.492, 1, Vaucluse. NEW ZEALAND, North Island, all from the Bay of Islands and deposited in ANSP; WAS-NZ 11 and 12, 1 specimen, N end of smaller island, just NW of Urupukapuka Id.; WAS-NZ 5, 1, SE side above small island; WAS-NZ 1, 14 (2 removed for clearing and staining), S end Urupukapuka Id.

Description: Counts and measurements summarized in tables 1 to 5. Body moderately elongate, depth at vent 4.5 to 6.9 in standard length. Body depth greatest at dorsal fin origin, tapering gradually to tail. Greatest body width behind head. Predorsal distance 3 to 4 times in standard length. Anal fin base origin at, or posterior to, midpoint of body. Ventral fins originating posterior to symphysis of cleithra by distance about equal to interorbital space. Pectoral fin 6.2 to 7.9 in standard length, extending at most to point one-half distance from pectoral fin upper angle to anal fin origin.

Scales on body non-imbricate, widely scattered; buried beneath a mucous coat on most specimens; apparently lacking on specimens less than about 30 mm SL. Scales absent on head; however, 1 Australian specimen, I. 12658, with rounded, pitlike structures on head, which resemble empty scale pockets more posteriorly on body. In the original description of *D. macrodon*, Ogilby mentioned scattered scales on the head. Frank Talbot examined the holotype for me and was unable to find either scales or scale pockets on the head.

Eye small, 8 to 14 times in head length, sunk beneath the surface. Most specimens with clear space in skin over eye, about equal in diameter to part of lens protruding through iris; few specimens with clear space over eye larger; eye completely covered with translucent skin in some specimens.

Posterior region of maxillary slightly or not at all sheathed. Prominent toothlike structure projecting down from maxillary at about level of rear margin of eye.

Gill rakers on first gill arch short, stubby, spiny tubercles; 3 or 4 longest on lower arm near angle; anteriorly along gill arch rakers are represented only by spiny bumps.

Premaxillary with band of short, sharply pointed teeth; band extending posteriorly to below eye; several longer teeth near anterior end of premaxillary. Vomer bearing V-shaped patch of unequal sized teeth. Similar teeth on palatines. Dentary bearing broad patch of small teeth anteriorly, similar to premaxillary teeth; extending posteriorly from each patch a single line of widely spaced large teeth interspaced with smaller teeth. No sexual dimorphism in dentition. Small specimens have notably fewer teeth than do large specimens; however, the general pattern of tooth distribution is similar in large and small fish.

The male genitalia (Fig. 2 B) consist of a fleshy hood, a curved papilla or penis which has fleshy, glandular (?) tissue attached to it, and two hard recurved claspers which extend posteriorly and at their distal ends turn laterally or posterolaterally. The claspers are flattened elongate structures. Sizes of papillae and claspers vary considerably; however, the claspers of specimen no. IB 7338 (Australia) are atypical and warrant special comment. They are large, flattened structures which

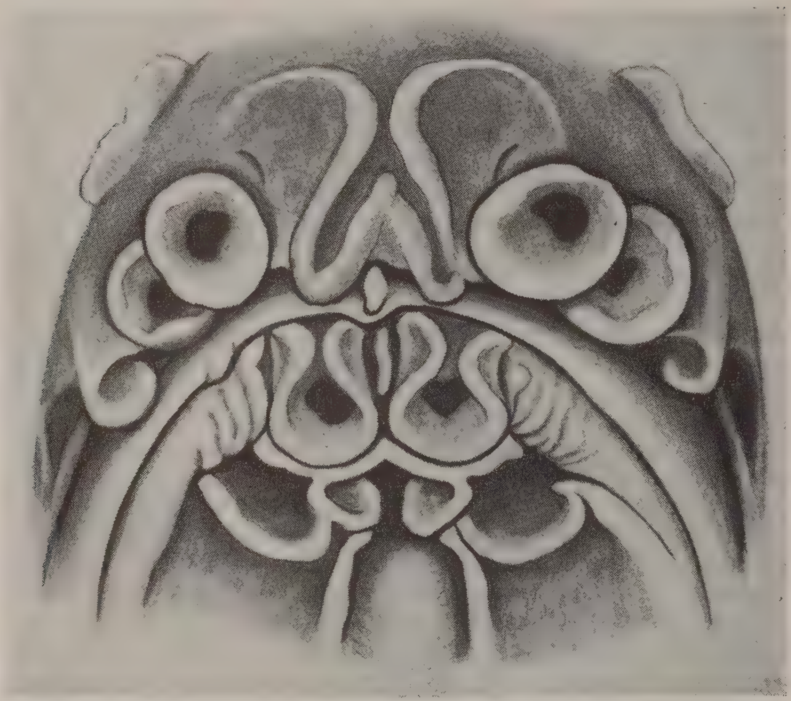


FIG. 3. *Dermatopsis macrodon.* AM IB 492 (see text for data). Anterior view of snout, slightly elevated, showing position of skin folds, pores, and nostrils. Drawn by Mildred H. Carrington.

project posteriorly and then dorsally beyond the margin of the genital hood. This specimen seems to be a typical *D. macrodon* in other respects, and I assume that its claspers are anomalous.

The distribution of lateralis system pores on the head (Fig. 3) is similar in Australian and New Zealand specimens. The lateral canal has a single pore near the upper angle of the gill opening. The supraorbital canal has 2 to 3 pores; one on the edge of the upper lip in front of the anterior nostril, a second, higher on the snout, on the inner edge of a circular ridge of skin surrounding an area of very thin skin, and a third, quite small and not always visible, above and behind the eye. The suborbital canal has 5 pores, 3 in the convoluted skin along the upper lip on the snout, and 2 along the skin over the maxillary behind the level of the eye. The preoperculo-mandibular canal has 7 or 8 pores, 3 in the convoluted skin folds near the lower jaw tip, the others evenly spaced along the inner margin of the ramus of the dentary and the preopercle; the last pore position in the series usually bears 2 pores, sometimes 1. Minute lateral line organs are visible along the sides of only a few specimens. They are in the form of a row of delicate papillae which originate near the upper angle of the gill slit. The lateral line extends posteriorly above the midline of the body as a row of about a dozen papillae. It descends to the midline slightly posterior to the level of the adpressed pectoral fin and extends to the caudal base as a row of another dozen papillae.

Vertebrae 1 to 5 have ribs articulating with the centra; those on 3 to 5 are pleural ribs; ribs on centrum 3, and to a lesser degree, on 4 are proximally flattened and bladelike; centra 6 to 13 have pleural ribs at ends of parapophyses. Epipleurals associated with pleural ribs on vertebrae 3, 4, 5, and sometimes 6. Thirteen abdominal vertebrae. Ribs on first 2 centra directed posteriorly, unlike pleural ribs on subsequent centra, which are directed ventrally or posteroventrally. The distal ends of the first 2 ribs are in line with the epipleurals of the following ribs. The two sides of the first neural spine are not fused. The above description is based on two cleared and stained specimens, one male and one female, from WAS-NZ 1, and on radiographs of all specimens.

All of the New Zealand specimens are uniformly pale. Some of the Australian specimens are pale anteriorly and dark brown posteriorly. Many specimens are covered with a thick mucous coating which contains many small granules.

Variation: D. macrodon is now known from New Zealand as well as New South Wales. It is to be expected that two populations of a shallow water species separated by 1200 miles of open water will show some morphological differences. Although my material is limited, I find three such differences: (1) Vertebral count—Australian range 39–42, New Zealand range 42–45. See table 5 for frequency distribution. (2) Body depth at vent—8 Australian specimens 30.0 to 57.9 mm SL, body depth ranges from 14.5 to 17.6 percent SL (average 16.3 percent); 8 New Zealand specimens 34.2 to 55.8 mm SL, body depth ranges from 16.7 to 22.3 percent SL (average 18.2 percent); (3) A characteristic feature of most New Zealand specimens, regardless of sex, is the presence of a pronounced rise in the dorsal profile between the rear of the head and the dorsal fin origin (Fig. 2 A). Most Australian specimens have only a gentle upward slope in this region.

Dermatopsis multiradiatus McCulloch and Waite

Figs. 4A, 4B

Dermatopsis multiradiatus McCulloch and Waite, 1918, p. 63, pl. 5, Fig. 4 (orig. descr., Kangaroo Id.).—Hubbs, 1938, p. 289 (discussion).—Scott, 1962, p. 172, Fig. (descr., Kangaroo Id., Cape Jervois).—Mees, 1962, p. 27 (head of Great Australian Bight).

?*Dipulus caecus* Waite, Thines, 1960, p. 45, pl. 1 (discussion of eye).

Dermatopsis caecus (Waite) in part, Mees, 1962, p. 27 (Rottnest Id.; Pt. Quobba, N of Shark Bay, Western Australia).

Diagnosis: A *Dermatopsis* with 98 to 114 dorsal rays, 64 to 72 anal rays, 51 to 55 vertebrae, and depth at vent 8.5 to 11.4 times in standard length.

Study material: AUSTRALIA, WESTERN AUSTRALIA, Rottnest Island, east end of Nancy Cove, WAM P.12712–P.12736, 23 specimens; SOUTH AUSTRALIA, Head of Bight, S of Nullarbor, WAM P.4461, 3 specimens.

Description: Counts and measurements summarized in tables 1 to 5. Body elongate, depth at vent 8.5 to 11.4 times in standard length. Body depth greatest along trunk, between nape and vent, tapering gradually from level of vent to caudal peduncle. Greatest body width behind head. Predorsal distance 4 to 5 times in standard length. Anal fin base origin near midpoint of body. Ventral fins originating posterior to symphysis of cleithra by distance slightly less than interorbital width. Pectoral fin 8.5 to 12.7 in standard length, extending one-third to one-fourth distance from pectoral fin upper angle to anal fin origin.

Scales generally non-imbricate, not widely scattered, hidden beneath thick mucous coating and finely punctulate epidermal layer. It is necessary to scrape away congealed mucus and use a compressed air jet on the cleared area before scales can be seen. Scales lacking on head.

Eye small, 10 to 18 times in head length, sunk beneath the surface; eye visible through clear place in skin. In South Australian specimens the lens is opaque white whereas in Western Australian examples it is translucent blue. It seems likely that difference in color is related to preservative as each collection also contains a specimen of *Dinematichthys* with lenses colored like the *Dermatopsis* in the same collection. Thines (1960) studied the eye of a fish which he called *Dipulus caecus* and which may be identical with the species here discussed. He noted that the eye of this fish represents an example of "simple microphtalmy" [sic] rather than true regression.

Dorsal rim of maxillary free at its distal extremity, elsewhere sheathed. There is a blunt, toothlike, ventral projection from the maxillary at about the level of the rear margin of the eye.

Gill rakers low, spiny tubercles, as many as 6 or 7 along lower arm of first gill arch.

Premaxillary with band of short, sharply pointed teeth; band extending posteriorly to beneath posterior nostril. Vomer with triangular patch of teeth similar to premaxillary teeth; in some specimens a few larger teeth present. A band of similar teeth present on palatine. Dentary bearing anteriorly a granular patch of smaller teeth. On inner edge and extending posteriorly from this patch a single line of larger, conical teeth. No sexual dimorphism in dentition.

Male genitalia (Fig. 4 B) consisting of a fleshy hood, a papilla with a strongly recurved tip, which has fleshy, glandular (?) tissue attached to it, and two hard recurved claspers which turn laterally at almost right angles.

Lateral canal with a single pore near the upper angle of the gill opening. Supraorbital canal with 2 pores in the specimen from Western Australia and 3 in South Australian specimens. Fishes from both

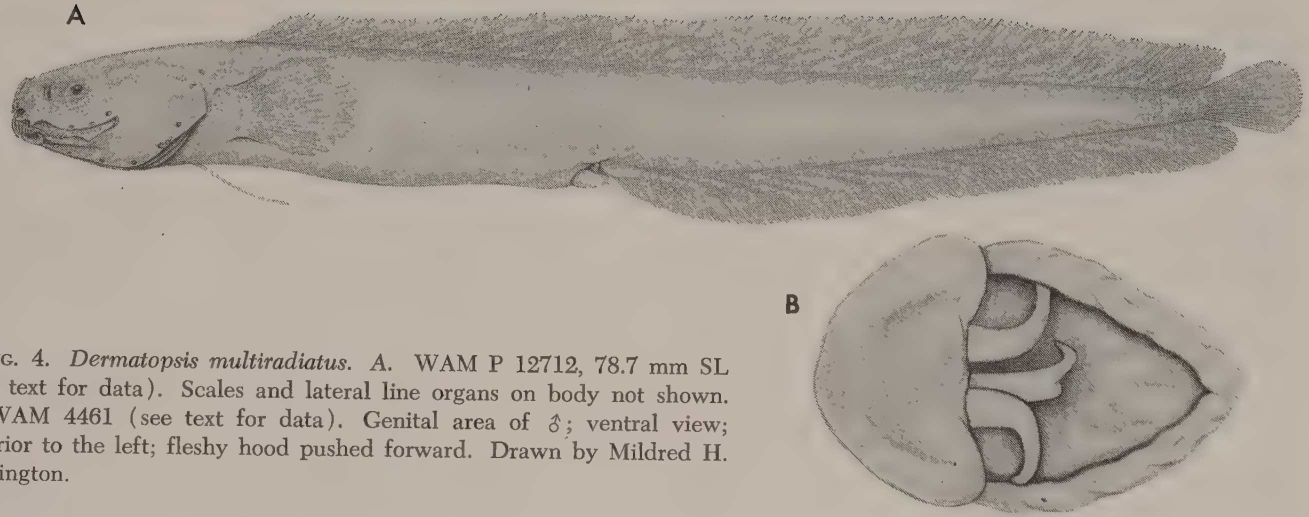


FIG. 4. *Dermatopsis multiradiatus*. *A.* WAM P 12712, 78.7 mm SL (see text for data). Scales and lateral line organs on body not shown. *B.* WAM 4461 (see text for data). Genital area of ♂; ventral view; anterior to the left; fleshy hood pushed forward. Drawn by Mildred H. Carrington.

localities have a pore in the flesh of the upper lip medial to the anterior nostril, and another behind the tube of the anterior nostril on the margin of a semicircular ridge of skin surrounding an area of very thin skin. A third pore of this series, present only in the South Australian specimens, is above and behind the eye. The suborbital canal has 6 pores, 3 in the convoluted skin along the upper lip on the snout and 3 along the skin over the maxillary behind the level of the anterior margin of the eye. The preoperculo-mandibular canal has 9 pores, 3 in the convoluted folds of skin near the lower jaw tip and the others along the inner margin of the ramus of the dentary and the preopercle; pores number 7 and 8 immediately adjacent to each other. The lateral line system along the side of the body is visible in a few specimens only. It consists of an upper section of about a dozen delicate papillae extending posteriorly from near the upper angle of the gill slit to about two-thirds the distance from the rear of the head to the vent, and a lower section of 25 to 30 papillae extending from the level of the termination of the upper line to the caudal fin base.

Vertebrae 1 to 5 have ribs articulating with the centra (based on radiographs). Subsequent abdominal centra have parapophyses, many of which bear ribs. The ribs are slight structures and do not show well on radiographs, and I cannot say whether they are present at the ends of all parapophyses. The two sides of the first neural spine are not fused.

The color is orange-brown; the South Australian specimens are slightly paler. A thick mucous coating, in which is embedded small orange granules, covers both the body and head. Beneath the mucous coating are numerous small, dark chromatophores which are externally visible only near the caudal fin base and along the dorsal fin base.

Variation: Mees (1962) referred South Australian and Western Australian material to different species, although he suggested they might represent subspecies rather than species. He listed three differences between the populations: degree of squamation and relative body depth (both of which I have been unable to verify) and color—possibly a function of preservation. The previously noted presence of a pore above and behind the eye in the South Australian specimens and its absence in the Western Australian material is the only character I have found which separates the material examined. As I have only three specimens in my South Australian sample, I prefer to consider the two populations conspecific.

Genus *Dermatopsoides*

Dermatopsoides Smith, 1947, p. 361 (type-species by original designation *Dermatopsis kasougae* Smith, 1943).

Diagnosis: Chin barbel absent. Gill membranes attached anteriorly to isthmus. Livebearing; male genitalia consisting of fleshy hood, two rounded, recurved, ossified claspers directed dorsally at their distal ends, and a penis. Pelvic fins immediately adjacent to each other, each with single ray, fins not originating immediately behind symphysis of cleithra but placed about an interorbital distance behind. Caudal fin with 16 or more rays, not joined with dorsal and anal fins although in some specimens short membranes may reach between bases of dorsal and anal fins and caudal fin; pectoral fin entire, without separate, elongated rays. Scales lacking or widely scattered on head and non-imbricate or absent on body. No spine on opercle. Anterior nostril tubular, located directly above upper lip; gill rakers reduced. Branchiostegal rays 6. Lateral line consisting of very small dermal papillae (difficult to see in some specimens). Teeth present on premaxillary, vomer, palatine, and dentary; maxillary elongated posteriorly but not vertically expanded, sheathed in a fold of skin distally. Eyes small. Peritoneum pale.

First neural spine shortest; neural spines on abdominal centra with sharp tips. Vertebrae 1 through 5 or 6 with ribs articulating with centra; parapophyses beginning on centrum 6 or 7.

Species: Two species are known, both from South Africa. One is herein described for the first time. The distribution of these species falls within the region which Stephenson (1947, Fig. 2) assigned to the warm temperate Cape fauna; more specifically, they are probably part of his south coast (Stephenson, 1947, pl. 16) component. Smith (1946, Fig. 1) showed the distribution of South African clinids, and his list included four species with an even wider distribution than *D. talboti.*

Dermatopsoides talboti, new species

Figs. 5A, 5B

Dermatopsoides kasougae Smith, 1949, p. 361, in part (brief description, Port Alfred to Bushman's River, Cape; *D. kasougae* is known only from the holotype; other specimens are *D. talboti.*

Diagnosis: A species of *Dermatopsoides* with no scales, 59 to 80 dorsal fin rays, 36 to 54 anal fin rays, and 17 to 18 pectoral fin rays. The eye goes into head length more than 15 times and the pelvic fin is no more than half the head length and does not extend beyond the posterior end of the pectoral fin.

Study material: SOUTH AFRICA, holotype, RU B. 59, ♂, 40.4 mm SL, Bird Island, Algoa Bay. Paratypes, RU B. 59, 1 spec., data as for holotype; SAM 21800, 1 spec., Somerset Strand, False Bay; USNM 199732, 1 spec., Simonstown, False Bay; SAM 21493, 1 spec., Saldanha Bay; SAM 21693, 1 spec., no data.

Description: Counts and measurements in tables 1 to 5. Body moderately elongate, depth at vent 5.8 to 8.3 in SL. Body depth about equal from level of nape to level of vent, tapering to tail. Greatest body width in region of belly between nape and vent, tapering thence to tail.

Dorsal fin origin on anterior third of body; anal fin origin posterior to midpoint of body. Vertical fins of some specimens covered with translucent skin, individual fin rays not easily visible; on other specimens skin over fins clear. Dorsal and anal fins not continuously connected with caudal fin along their entire heights; however, membranes may be present at bases of last dorsal and anal rays connecting them with the caudal peduncle, or in some fish, with bases of dorsal and ventral rays of caudal fin. Caudal fin rounded. The single ray of each pelvic fin thick proximally, but tapering to filamentous tips which do not extend beyond level of posterior end of pectoral fin; pelvic fins originating posterior to symphysis of cleithra by a distance about equal to interorbital space. Pectoral fins inserted vertically on broad muscle pad; fins 6.4 to 8.1 in SL, extending about one-half of distance from pectoral fin upper angle to vent.

Eye tiny, skin-covered, sunk beneath surface of head, 16 to 30 times in head. A chromatophore-free porthole, in some specimens transparent, in others translucent, covering eye.

Head compressed, deeper than wide. Posterior nostril in front of eye, with raised, fleshy rim; short, tubular anterior nostril at anterolateral corner of snout immediately above lip.

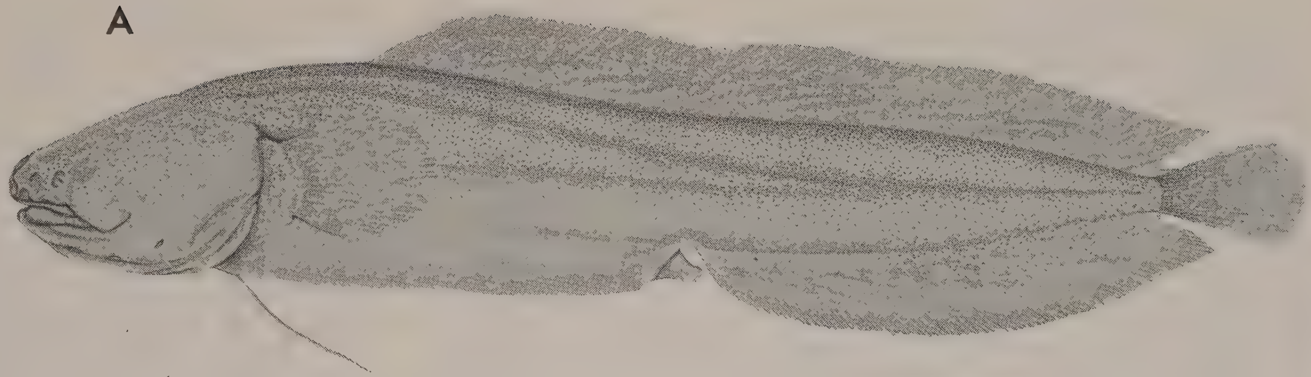
Maxillary elongated posteriorly, not vertically expanded; posterior projection almost completely sheathed. The crease between snout and upper jaw interrupted by a broad frenum connecting suborbital area with anterior part of maxillary.

Gill rakers short, stubby tubercles, 3 or 4 on the upper arm of first arch and as many as 8 or 9 on lower. Tubercles progressively smaller anteriorly on each arm.

Premaxillary bearing short, pointed teeth which extend posteriorly in a line reaching only to level of anterior margin of eye. Cluster of similar teeth present at symphysis of dentaries; row of 8 to 10 larger pointed teeth extending posteriorly along dentary. Vomer with broadly V-shaped band of about 10 pointed teeth; about 8 or 9 similar teeth extending posteriorly in single row along palatines. No sexual dimorphism in dentition.

Male genitalia (Fig. 5 B) consisting of a fleshy hood; an elongate papilla or penis which has fleshy, glandular (?) tissue attached to it; and two hard, recurved claspers. The claspers extend posteriorly and turn dorsally at their distal ends.

The lateralis system is difficult to see, and only a few observations were possible. The lateral canal has a single pore, near the upper angle of the gill opening; the supraorbital canal apparently has a single pore, on the snout near the anterior nostril; the infraorbital canal has at least 5 pores, including 2 very large ones on the snout; and the preoperculomandibular canal appears to have at least 6 or 7 pores, including some very large ones with fleshy, convolute margins near the lower jaw tip. Small and inconspicuous papillae mark the course of the lateral line along the body. The line originates near the upper angle of the opercle and descends to the midline of the body between the level of the posterior end of the pectoral fin and the level of the vent. One speci-



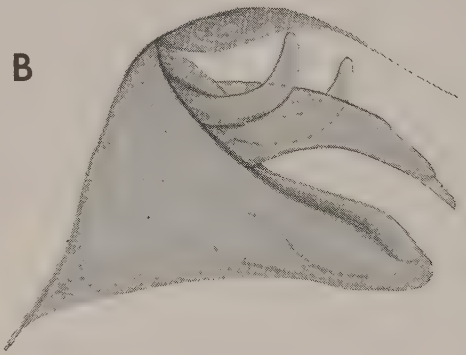


FIG. 5. *Dermatopsoides talboti*. *A*. RU B. 59; holotype; 40.4 mm SL (see text for data). Lateral line organs on body not shown; some head pores not shown. *B*. RU B. 59; ♂ holotype; genital area; lateral view; anterior to the left; fleshy hood pushed slightly forward. Drawn by Mildred H. Carrington.

men had about 20–25 papillae, another had 23. Papillae were not visible in the other specimens.

Vertebrae 1 to 5 have ribs articulating with the centra; 6 to 10, 11, or 12 have pleural ribs at the ends of parapophyses. Epipleurals are associated with at least some ribs; however, precise observations were not possible from radiographs.

Preserved specimens are pale. Small, dark chromatophores are distributed along the dorsal part of the head and trunk and on the side of the body behind the level of the vent. An entry in the fish catalog of the South African Museum noted that specimen number 23256 was "red in color."

Variation: The considerable meristic variation among specimens from widely separated localities suggests that when additional material is available subspecies may be demonstrable. The two specimens from Bird Island (at the east end of Algoa Bay) are geographically closer to the known locality for *D. kasougae*. However, they are meristically quite widely separated from it, while the west coast Saldanha Bay specimen of *D. talboti*, which is geographically farthest from the type-locality of *D. kasougae*, is closest to it in counts.

Dermatopsoides kasougae (Smith)

Dermatopsis kasougae Smith, 1943, p. 72, Fig. 3 (orig. descr.).

Dermatopsoides kasougae Smith, 1947, p. 344 (new genus proposed).—Smith, 1949, p. 361, *in part* (brief descr., Port Alfred to Bushman's River, Cape; *D. kasougae* is known only from the holotype, the other specimens mentioned are *D. talboti*).

Diagnosis: A species of *Dermatopsoides* with non-imbricate scales on body, 100 dorsal fin rays, 71 anal fin rays, and 24 pectoral fin rays. The eye goes about 10 times in head length, and the pelvic fin is more than half the head length and extends beyond the posterior end of the pectoral fin.

Study material: The holotype, a male, from the mouth of the Kasouga River, west of Port Alfred.

Description: Counts and measurements in tables 1 to 5. The single known specimen is in poor condition, and I can add only a few items to the original description.

Although not shown in the original figure of the holotype, there are, as Smith noted in his written description, membranes connecting the bases of the posteriormost dorsal fin ray with the dorsalmost caudal fin ray and the posteriormost anal fin ray with the ventralmost caudal fin ray. Smith described the distribution of scales as follows, "The head is entirely naked. Minute very indistinct cycloid scales buried in a thick dermal layer over the whole body to the nape. It is only on the nape that they appear to be slightly diffuse, but as far as may be observed, on the rest of the body they are normally and regularly imbricate." I have examined the squamation using a compressed air jet, and I find the scales everywhere non-imbricate. They are more widely scattered and more deeply embedded on the nape. C. Dawson examined the holotype and pointed out to me structures in the interorbital area which he believes to be scales or scale pockets. On the basis of the condition in this single specimen I prefer not to comment on whether the head has scales. Vertebrae 45.

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TABLE 1. Summary of proportional measurements on dermatopsine fishes.

	Dermatopsis macrodon						*Dermatopsis multiradiatus*				*Dermatopsoides*			
	Australia			New Zealand			S. Aust.	W. Aust.			*kasougae*	*talboti*		
	$\bar{x}$%	Range%	*N*	$\bar{x}$%	Range%	*N*	%	$\bar{x}$%	Range%	*N*	%	$\bar{x}$%	Range%	*N*
Standard length		30.0–68.5			25.1–55.9		74.9		52.0–95.8		63.3		26.6–50.9	
Head length	22.6	21.2–25.3	8	22.7	21.5–24.3	8	16.3	17.4	15.9–20.2	17	24.0	23.3	22.0–26.7	6
Eye diameter	2.2	1.7–2.7	7	2.4	2.1–2.8	8	1.1	1.2	1.0–1.6	14	2.4	1.1	0.74–1.4	6
Snout length	5.5	4.7–7.0	7	5.9	5.3–6.8	8	4.1	3.5	2.8–4.1	17	4.3	5.0	4.3–5.3	6
Postorbital length	15.9	15.1–17.3	7	15.4	14.7–16.1	8	10.3	12.0	10.5–13.4	17	13.6	16.4	14.7–17.8	6
Predorsal length	29.2	27.9–31.0	6	30.4	28.4–33.0	7	21.4	22.6	20.3–24.9	17	26.2	31.0	28.5–33.1	5
Preanal length	53.6	50.6–55.8	8	51.3	50.5–52.3	7	53.0	51.4	48.1–54.0	17	49.9	55.2	52.2–59.5	5
Preventral length	18.5	17.4–20.4	7	19.5	16.6–22.5	8	13.8	13.8	12.3–15.2	17	17.1	19.2	17.1–21.8	6
Body depth	16.4	14.5–17.6	7	18.1	16.7–22.3	7	11.3	10.2	8.8–11.7	14	16.3	14.6	12.0–17.2	5
Pectoral length	13.5	11.2–16.3	6	13.9	12.6–15.7	6	8.3	9.4	7.9–11.3	15	11.8	13.9	12.4–15.3	6
Ventral fin length	12.9	11.2–16.0	7	13.9	12.3–14.9	8	7.9	10.0	7.5–14.1	15	18.8	11.6	7.9–13.4	4

TABLE 2. Frequency distribution of dorsal fin ray counts in dermatopsine fishes.

	Dermatopsis macrodon		*Dermatopsis multiradiatus*		*Dermatopsoides*	
	Australia	New Zealand	S. Australia	W. Australia	*kasougae*	*talboti*
Dorsal rays						
59						1
60						1
61						
62						
63						
64						1
65						1
66						
67						1
68						
69						
70						
71	2					
72						
73	1					
74		2				
75	2	2				
76		3				
77	1					
78		1				
79		2				
80	1	2				1
98				1		
99						
100					1	
101						
102						
103						
104				2		
105			1	2		
106			1	2		
107				3		
108				1		
109				2		
110				1		
111			1			
112						
113						
114				1		

TABLE 3. Frequency distribution of anal fin ray counts in dermatopsine fishes.

	Dermatopsis macrodon		*Dermatopsis multiradiatus*		*Dermatopsoides*	
	Australia	New Zealand	S. Australia	W. Australia	*kasougae*	*talboti*
Anal rays						
36						1
37						
38						
39						
40						
41						
42						1
43						
44						3
45	1					
46						
47						
48						
49	2					
50	1	1				
51	1	2				
52	1					
53	1	3				
54		1				1
55		3				
56	1					
57		2				
58						
59						
60						
61						
62						
63						
64			1	1		
65			1			
66			1			
67				1		
68				3		
69				3		
70				3		
71				3	1	
72				2		

TABLE 4. Frequency distribution of pectoral fin ray counts in dermatopsine fishes.

	Dermatopsis macrodon		*Dermatopsis multiradiatus*		*Dermatopsoides*	
	Australia	New Zealand	S. Australia	W. Australia	*kasougae*	*talboti*
Pectoral rays						
17						5
18						1
19		4		1		
20	1	4	2	1		
21	4	4		5		
22	1			12		
23	1			2		
24					1	

TABLE 5. Frequency distribution of vertebrae in dermatopsine fishes.

	Dermatopsis macrodon		*Dermatopsis multiradiatus*		*Dermatopsoides*	
	Australia	New Zealand	S. Australia	W. Australia	*kasougae*	*talboti*
Vertebrae						
37						1
38						1
39	1					3
40	1					
41	3					
42	3	2				
43		10				1
44						
45		2			1	
46						
47						
48						
49						
50						
51			1			
52						
53			1	6		
54			1	7		
55				4		

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THE NORTH PACIFIC DEEPSEA FISH NAME *BATHYLAGUS MILLERI* GILBERT, A SENIOR SYNONYM OF *BATHYLAGUS ALASCANUS* CHAPMAN.–Among the eastern Pacific species of *Bathylagus* with a restricted gill slit, an elongate anal fin base, and dark pigment are two well-differentiated species that have three names in current usage: *Bathylagus pacificus* Gilbert, 1890; *Bathylagus milleri* Jordan and Gilbert, 1898 (in Jordan and Evermann, 1898); and *Bathylagus alascanus* Chapman, 1939. The proper allocation of these names has long been a source of disagreement. Some authors have considered *B. milleri* as a junior synonym of *B. pacificus*, while others have treated *B. milleri* as a senior synonym of *B. alascanus*. I have studied the type material of all three nominal species. The holotype of *B. milleri* is badly mutilated and observations were possible on only two of the many characters that separate *B. pacificus* from "the other species." These are numbers of pectoral fin rays and vertebrae. I have made counts on specimens of the two species in the collections of the U. S. National Museum, the California Academy of Sciences, Stanford University, and Scripps Institution of Oceanog-

TABLE 1. PECTORAL FIN RAYS IN *Bathylagus milleri* AND *B. pacificus*.

Fin Rays	*B. milleri*	*B. pacificus*
7		1
8		2
9		35
10		8
11		1
12	3[1]	
13	10	
14	13	
15	9[2]	
16	1	

[1] Holotype of *B. milleri*.
[2] Holotype of *B. alascanus*.

TABLE 2. VERTEBRAE (NOT INCLUDING UROSTYLE) IN *Bathylagus milleri* AND *B. pacificus*.

Vertebrae	*B. milleri*	*B. pacificus*
44		5
45		6[3]
46		4
47		4
48		2
49		
50	3[1]	
51	6[2]	
52	2	
53	–	
54	2	

[1] Holotype of *B. milleri*.
[2] Holotype of *B. alascanus*.
[3] Holotype of *B. pacificus*.

raphy, and have summarized my data in Tables 1 and 2. On the basis of these data *B. milleri* and *B. alascanus* are conspecific.

When Chapman (1939) described *B. alascanus* he considered the possibility that it might be identical with *B. milleri*. One of his characters for distinguishing the two species was the presence in the interorbital space of *B. milleri* of "two vertical thin lamellae which arise on either side, and mark off the narrow interorbital space from the contiguous supraocular areas." These structures are readily identifiable on the bare skull bones of the holotype of *B. milleri*. Chapman stated that in specimens of *B. alascanus*, on the other hand, the interorbital was concave or flat. I have found, however, that specimens of "*B. alascanus*" (including a paratype) have vertical thin lamellae in the interorbital, identical with those on the holotype of *B. milleri*. To observe these structures, however, it is necessary to dissect away some of the soft tissue that constitutes the surface of the concave or flat interorbitals of the type material of *B. alascanus*. Chapman also mentioned that, "In *B. milleri* the occiput is swollen and prominent, much higher than the interorbital space. In *B. alascanus* the occiput is normal." The fact that the holotype of *B. milleri* has lost all of the fleshy cover from its interorbital area makes the occiput appear relatively more prominent.

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A Review of the Venomous Toadfishes, Subfamily Thalassophryninae

BRUCE B. COLLETTE

A Review of the Venomous Toadfishes, Subfamily Thalassophryninae

BRUCE B. COLLETTE

The subfamily Thalassophryninae differs from the other two subfamilies of Batrachoididae (Batrachoidinae and Porichthyinae) in having two hollow dorsal spines and a hollow opercular spine that connect with venom glands. *Thalassothia* Berg is shown to be a synonym of *Thalassophryne* Günther. The eastern Pacific *Daector* Jordan and Evermann differs from the western Atlantic *Thalassophryne* in having discrete glands between the bases of the upper pectoral fin rays and in having more precaudal and caudal vertebrae and more second dorsal and anal fin rays. Three species of *Daector* are recognized: *reticulata* Günther; *gerringi* Rendahl; and *dowi* Jordan and Gilbert (including *depressa* Hildebrand). Six species of *Thalassophryne* are recognized: *amazonica* Steindachner; *megalops* Bean and Weed; *maculosa* Günther (including *quadrizonatus* Eigenmann and *wehekindi* Fowler); *nattereri* Steindachner (including *branneri* Starks); *punctata* Steindachner; and *montevidensis* Berg (including *platensis* Devincenzi).

The presence or absence of the axillary and pectoral fin glands are considered to be of generic value. *Thalassophryne, Amphichthys,* and *Halophryne* lack both glands. *Daector, Aphos, Porichthys,* and *Batrachoides* lack the axillary gland but have discrete pectoral fin glands. *Batrachomoeus* and *Sanopus* have the axillary gland and lack pectoral fin glands. *Opsanus* has both types of glands. *Opsanus astrifer* is placed in *Sanopus* along with *O. barbatus.*

INTRODUCTION

TOADFISHES of the subfamily Thalassophryninae (family Batrachoididae) have the most highly developed venom apparatus of any fishes. The two dorsal spines and the opercular spines are hollow tubes leading out from venom glands. Other groups of venomous fishes have only grooved spines. Descriptions of the venom apparatus have appeared numerous times in the literature (Günther, 1864b, 1869, 1880; Gill, 1907; Pellegrin, 1908; Bean and Weed, 1910;

Phisalix, 1922) but the species remain little known. The subfamily is limited to the continental shelves of the eastern Pacific and western Atlantic oceans. Of the 14 nominal species, 7 are known only from the original descriptions. Only two of the species, *Daector dowi* and *D. reticulata*, have been commonly reported. The purposes of this paper are to determine the number of valid genera and species, and to report on recently collected material of most of the species.

MATERIALS

Material of all valid species of the subfamily has been examined. Types of all nominal species except *T. amazonica* Steindachner and *T. quadrizonata* Eigenmann have been studied. The latter two types are apparently lost. The specimens examined have come from the following 25 institutions, whose curatorial staff members have been of great assistance:

ANSP—Academy of Natural Sciences of Philadelphia (Dr. James E. Böhlke); BMNH—British Museum (Natural History) (Dr. P. H. Greenwood); CAS—California Academy of Sciences, San Francisco (Mr. W. I. Follett); CU—Cornell University, Ithaca, New York (Dr. Edward C. Raney); EPN—Escuela Politecnica Nacional, Quito, Ecuador (Dr. Gustavo Orcés Villagomez); FMNH—Field Museum of Natural History, Chicago (Miss Pearl Sonoda); IMARPE—Instituto del Mar del Peru, La Punta, Peru (Srta. Norma Chirichigno F.); LACM—Los Angeles County Museum (Mr. Robert Lavenberg); MACN—Museo Argentina de Ciencias Naturales (Dr. Rogelio B. Lopez); MBUCV—Museo de Biologia, Universidad Central de Venezuela, Caracas (Sr. Francisco Mago Leccia); MNRJ—Museu Nacional, Rio de Janeiro (the late Dr. Paulo de Miranda Ribeiro); MCZ—Museum of Comparative Zoology, Harvard University (Dr. Giles W. Mead); MNHN—Muséum National d'Histoire Naturelle, Paris (Mme. M. L. Bauchot); MNM—Museo Nacional de Montevideo (Dr. Miguel Klappenbach); NMV—Naturhistorisches Museum, Vienna (Dr. Paul Kähsbauer); NRS—Naturhistoriska Riksmuseet, Stockholm (Prof. A. Johnels); RNH—Rijksmuseum van Natuurlijke Historie, Leiden (Dr. G. F. Mees); SIO—Scripps Institution of Oceanography, La Jolla (Dr. Richard H. Rosenblatt); SU—Division of Systematic Biology, Stanford University (Mr. Stewart Springer); TABL—Bureau of Commercial Fisheries Tropical Atlantic Biological Laboratory, Miami (Mr. Frederick H. Berry); UBC—Institute of Fisheries, University of British Columbia, Vancouver (Dr. C. C. Lindsey); UCLA—University of California, Los Angeles (Mr. Wayne J. Baldwin); UF—University of Florida, Gainesville (Dr. Carter R. Gilbert); UMML—University of Miami, Institute of Marine Science (Dr. C. Richard Robins); UPR—University of Puerto Rico, Institute of Marine Biology, Mayagüez (Dr. John E. Randall); USNM—U. S. National Museum, Washington.

Thalassophryninae

Members of the Thalassophryninae differ from all other toadfishes in having two hollow dorsal spines and a hollow opercular spine which lead out from venom glands.

Other distinguishing characters include: body scaleless; canine teeth absent; lateral line single; no photophores; no axillary gland; precaudal vertebrae 7 or 8, caudal vertebrae 19–32, total 26–40; dorsal rays 17–33, anal 16–30, pectoral 13–18.

Miranda-Ribeiro (1915) erected the family Thalassophrynidae for *Thalassophryne* and *Thalassothia* and the family Porichthyidae for *Porichthys*. Most subsequent authors (e.g., Hubbs and Schultz, 1939) retained all the toadfishes in the family Batrachoididae and did not use Miranda-Ribeiro's family names for subfamilies. Smith (1952:314–315), however, in the only recent key to the genera of Batrachoididae, recognized three subfamilies: Batrachoidinae, Porichthyinae, and Thalassophryninae. He included four genera in the latter subfamily: *Thalassophryne*, *Daector* Jordan and Evermann, *Thalassothia* Berg, and with question, *Triathalassothia* Fowler. Soriano Señorans (1958) and Ringulet and Arámburu (1960) pointed out that *Triathalassothia devincenzii* Fowler (1943: 331) is a junior synonym of *Amphichthys argentinus* (Berg), a member of the Batrachoidinae. I have confirmed this view by examination of both Fowler's holotype (ANSP 70373) and Berg's holotype (MACM 4592). *Thalassothia* Berg was based on a specimen of *Thalassophryne montevidensis* with the first two rays of the second dorsal fin broken, leading Berg and subsequent workers to believe that they were two additional dorsal spines.

The most significant character that separates the three eastern Pacific species (*Daector*)

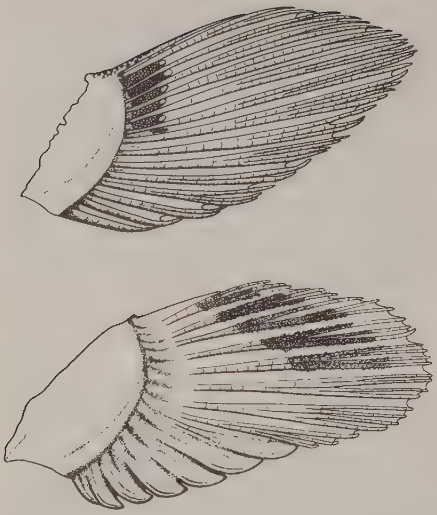

Fig. 1. Pectoral fins of *Thalassophryne* and *Daector*, posterior view. Upper: *D. dowi* showing discrete glands between the bases of the upper pectoral fin rays. Lower: *T. maculosa* showing glandular tissue scattered medially on the upper pectoral fin rays. The pectoral fin of *T. maculosa* is much fleshier therefore the ventral rays do not show through as well as in *D. dowi*.

of Thalassophryninae from the six western Atlantic species (*Thalassophryne*) is the presence of discrete glands between bases of the uppermost pectoral fin rays in *Daector* (Fig. 1). These glands are similar to those in *Opsanus tau* studied by Wallace (1893). To ascertain the generic value of the pectoral fin glands and the axillary gland in the Batrachoididae, I made a survey of the material in the collections of the U. S. National Museum. *Amphichthys* (two species) and *Halophryne diemensis* agree with *Thalassophryne* in lacking both the axillary gland and discrete pectoral fin glands. *Aphos porosus*, *Porichthys* (seven species), and *Batrachoides* (five species) agree with *Daector* in lacking an axillary gland but have discrete pectoral fin glands. *Batrachomoeus* (two species) and *Sanopus* (two species) have the axillary gland and lack discrete pectoral fin glands. *Opsanus* (four species) has both the the axillary gland and discrete pectoral fin glands.

Thus, the presence or absence of pectoral fin glands and of the axillary gland seems to be consistent within a genus. *Sanopus*, described by Smith (1952) for *Opsanus barbatus* Meek and Hildebrand, because *O. barbatus* has more dorsal and anal rays than the other species placed in *Opsanus*, further differs from *Opsanus* in lacking discrete pectoral fin glands. *Opsanus astrifer* Robins and Starck (1965) must also be placed in *Sanopus* because it lacks discrete pectoral fin glands and has a high number of dorsal and anal fin rays and vertebrae.

KEY TO THE SUBFAMILIES OF BATRACHOIDIDAE AND THE SPECIES OF THALASSOPHRYNINAE

1a. Dorsal spines three; subopercular spines present; body with or without scales; axillary gland present or absent .... Batrachoidinae
1b. Dorsal spines two; subopercular spines absent; body scaleless; axillary gland absent 2
2a. Dorsal and opercular spines solid with no venom glands under them; several lateral lines present; canine teeth present; pectoral glands present .... Porichthyinae
2b. Dorsal and opercular spines hollow with venom glands present under them; lateral line single or absent; canine teeth absent; pectoral glands present or absent .... Thalassophryninae 3
3a. No distinct glands present on pectoral fin; second dorsal rays 17–21; anal rays 16–20; Atlantic species .... *Thalassophryne* 4
3b. Three to seven distinct glands located between the bases of the uppermost pectoral rays; second dorsal rays 22–33; anal rays 21–30; Pacific species .... *Daector* 9
4a. Lateral line absent on head and body; dorsal and anal fins completely confluent with caudal; freshwater species .... *T. amazonica* (Fig. 2)
4b. Lateral line well developed on head and body; dorsal and anal fins separate from caudal; marine species 5
5a. Dorsal, anal, pectoral, and caudal fins pigmented to distal margins 6
5b. Dorsal, anal, pectoral, and caudal fins with pale distal margins 8
6a. No prominent spots on body or fins; pectoral fin rays 13–15, usually 14; eye very large, 54–67 ($\bar{x}$ 62) thousandths of standard length .... *T. megalops* (Fig. 5)

6b. Prominent spots all over body; pectoral fin rays 14–17, usually 15 or 16; eye smaller, 28–78 ($\bar{x}$ 31–54) thousandths of standard length 7

7a. Body pale with many uniformly small spots; eye very small, 28–33 thousandths of standard length; second dorsal rays 20–21; anal rays 19 .... *T. punctata*

7b. Body color variable with small and large spots, frequently with large blotches; eye moderately large, 37–78 ($\bar{x}$ 54) thousandths of standard length; second dorsal rays 17–20, usually 18; anal rays 16–19, usually 17 .... *T. maculosa* (Fig. 6)

8a. Second dorsal rays 19–20, usually 20; anal rays 18–20, usually 19; interorbital distance smaller, 46–74 ($\bar{x}$ 61) thousandths of standard length .. *T. nattereri* (Fig. 8)

8b. Second dorsal rays 18–19; anal rays 17–18; interorbital distance larger, 70–102 ($\bar{x}$ 83) thousandths of standard length .... *T. montevidensis* (Fig. 9)

9a. Second dorsal rays 29–33; anal rays 28–30; anal fin without dark stripe; second dorsal fin with dark distal margin .... *D. dowi* (Fig. 12)

9b. Second dorsal rays 22–28; anal rays 21–27; anal fin with dark submarginal stripe; second dorsal fin with or without dark submarginal stripe 10

10a. Dark submarginal stripe present in both dorsal and anal fins; pectoral fin glands 3; pectoral rays 15; second dorsal rays 28; anal rays 27 .... *D. gerringi* (Fig. 11)

10b. Dark submarginal stripe present only in anal fin; pectoral fin glands 6 or 7; pectoral rays 16–18; second dorsal rays usually 26; anal rays usually 25 .... *D. reticulata* (Fig. 10)

Thalassophryne Günther

Thalassophryne Günther, 1861:174 (original description, type-species *Thalassophryne maculosa* Günther, 1861 by monotypy).

Thalassothia Berg, 1895:66 (original description, type-species *Thalassophryne montevidensis* Berg, 1893 by monotypy).

Thalassophryne differs from *Daector* in the form of the pectoral fin glands and in having fewer vertebrae and dorsal and anal fin rays. The pectoral fin glands are not discrete structures with pores. Instead, glandular tissue is scattered along the upper several rays of the pectoral fin (Fig. 1). *Thalassophryne* has 7 precaudal vertebrae instead of 8 and 19–23 caudal vertebrae instead of 23–32 (Table 1); 17–21 second dorsal rays instead of 22–33 (Table 2); and 16–20 anal rays instead of 21–30 (Table 3). The number of second dorsal rays is two less than the number of caudal vertebrae instead of equal or only one less (compare Tables 4 and 5). *Thalassophryne* includes the six Atlantic species: *amazonica* Steindachner, *megalops* Bean and Weed, *maculosa* Günther, *nattereri* Steindachner, *punctata* Steindachner, and *montevidensis* Berg. The species are much less differentiated than those in *Daector*. Pigmentation differences seem to be important in distinguishing the species.

Thalassophryne amazonica Steindachner

Figs. 2, 3

Thalassophryne amazonica Steindachner, 1876:161–163 (original descripton; Brazil, Amazon River at mouth of Río Negro and at Tabatinga and Xingu). Meek and Hall, 1885:53–54 (after Steindachner). Ogilby, 1908:55 (listed). Bean and Weed, 1910: 517–518 (description after Steindachner). Miranda-Ribeiro, 1915:627–628 (after Steindachner). Fowler, 1931:405 (after Steindachner; comparison with *T. wehekindi*).

Types.—*T. amazonica* originally was based on at least three specimens deposited in the Vienna Museum, all of which are now apparently lost according to Dr. Paul Kähsbauer (pers. comm.). The types had the following counts according to Steindachner (1876): dorsal rays II-20; anal 18; and pectoral 13–14. The dorsal and anal fins were confluent with the caudal.

Diagnosis.—A small species of *Thalassophryne* known only from the fresh waters of the Amazon River. *T. amazonica* differs from all the other species of Thalassophryninae in lacking a prominent lateral line on the head and body (Figs. 2, 3). There are only a few scattered pores on the head and body. Both *T. amazonica* and *Daector dowi* have the dorsal and anal fins connected with the caudal fin, but the three fins are completely confluent in *T. amazonica* and only slightly connected in *D. dowi* (compare Fig. 2 with Fig. 12). In most counts, *T. amazonica* is similar to most of the Atlantic marine species: second dorsal rays 19–21; anal 18–19; pectoral 14–15; caudal vertebrae 20–21. *T. amazonica* has a smaller eye (26–40 thou-

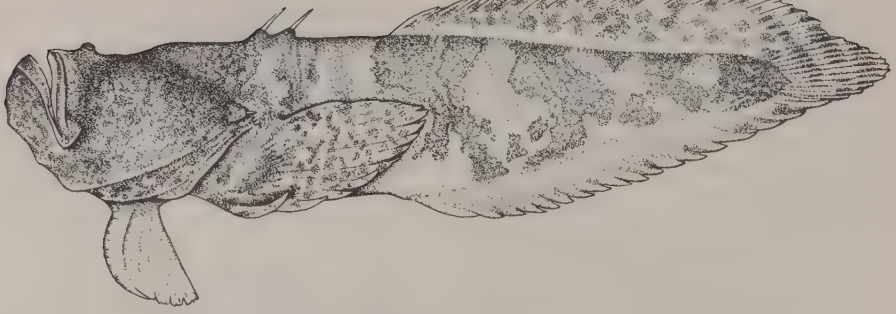

Fig. 2. *Thassophryne amazonica* Steindachner. USNM uncat. 68.2 mm SL, Peru, Río Itaya, a tributary of the Amazon north of Iquitos, Peru.

sandths of standard length) than any species of *Thalassophryne* except *T. punctata.* It has a greater interorbital distance (65–88 thousandths of standard length) than *T. punctata* but less than *T. montevidensis.*

Range.—Confined to the Amazon River and its tributaries (Fig. 4). Described by Steindachner (1876) from the mouth of Río Negro, and from Tabatinga and Xingu. Here recorded from Río Itaya near Iquitos, Peru and from Río Conambo and Río Corrientes in Pastaza Province, Ecuador.

Material examined.—USNM uncat. (2, 22.5–68.2), Peru, Río Itaya north of Iquitos, 25 Aug. 1965, F. Ancieta C. USNM 200560 (1, 57.9) and EPN uncat. (1, 73.7), Ecuador, Pastaza Province, Río Conambo, mouth of Río Shiona, Nov. 1960, R. Olalla. USNM 200559 (3, 37.3–92.9) and EPN uncat. (3, 32.3–67.2), Ecuador, Pastaza Province, Río Corrientes, March 1958, Herrera and Olalla.

Thalassophryne megalops Bean and Weed
Fig. 5

Thalassophryne megalops Bean and Weed, 1910:523–524 (original description; Gulf of Darien, Colombia). Meek and Hildebrand, 1928:921–922 (description after Bean and Weed). Rendahl, 1940:3 (after Bean and Weed; comparison with *T. gerringi*).

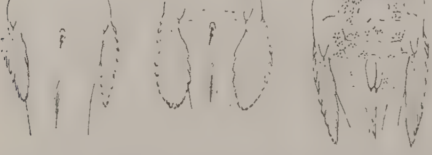

Fig. 3. Dorsal view of heads of *Thalassophryne amazonica, T. nattereri,* and *Daector reticulata* showing relative development of lateral line.

Types.—Holotype USNM 37669 (53.9 mm), Gulf of Darien, Albatross Station 2142, 9°31′ N, 76°20′ W, 42 fms, 23 March 1894. Paratype USNM 197643 (41.7 mm), removed from USNM 37669. Dorsal II-18, anal 17 in both; pectoral 13–13 in holotype and 14–14 in paratype; vertebrae 7 + 20 = 27 in both.

Diagnosis.—A small, rather dull species of *Thalassophryne* with four faint dark dorsal saddles (Fig. 5). In counts *T. megalops* is closest to *T. maculosa* and *T. montevidensis;* second dorsal rays 17–19, usually 18; anal rays 16–18, usually 17; caudal vertebrae 19–20, usually 20. *T. megalops* has a low number of pectoral rays (13–15, usually 14) similar to *T. amazonica* (13–14) and different from the other species of *Thalassophryne* (14–17, usually 15 or 16, Table 6). *T. megalops* has the largest eyes in the subfamily, 54–67 thousandths of standard length, and a very small interorbital distance (48–61 thousandths standard length, Table 7).

Range.—Known only from the Gulf of Darien off Colombia (type locality) and off Panama (recent Oregon collections) at depths of 42–100 fms (Fig. 4).

Material examined.—Panama. USNM 200556 (2, 35.7–51.9), Oregon 3594, 8°56′ N, 80°57′ W, 50 fms, 30 May 1962. TABL uncat. (5, 47.2–61.5), Oregon 3588, 9°18′ N, 80°27′ W, 100 fms, 29 May 1962. TABL uncat. (2, 56.5–62.9), Oregon 3589, 9°18′ N, 80°26′ W, 45 fms, 29 May 1962. USNM 187946 (19, 47.9–61.5), FMNH 66832 (1, 47.8), MCZ 45045 (2, 53.0–55.7), ANSP 103620 (2, 51.4–57.1), and TABL uncat. (5, 47.1–58.4), Oregon 3587, 9°18′ N, 80°25′ W, 75 fms, 29 May 1962.

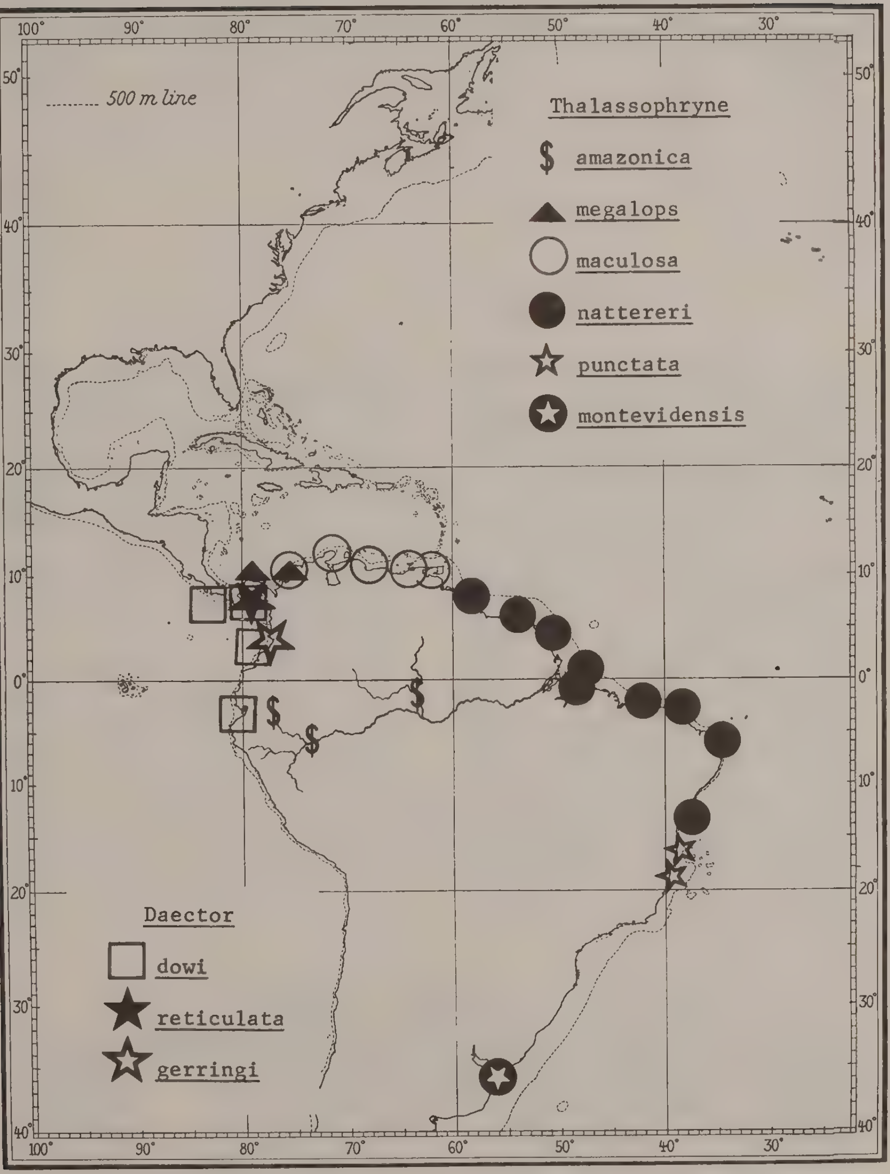
500 m line
Thalassophryne
amazonica
megalops
maculosa
nattereri
punctata
montevidensis
Daector
dowi
reticulata
gerringi
100°
90°
80°
70°
60°
50°
40°
30°
50°
40°
30°
20°
10°
0°
10°
20°
30°
40°

Fig. 4. General distribution of the species of *Thalassophryne* and *Daector*.

TABLE 1. NUMBER OF VERTEBRAE IN SPECIES OF THALASSOPHRYNINAE. (* Indicates counts of types.)

Species	Precaudal 7	8	Caudal 19	20	21	22	23	24	25	26	27	28	29	30	31	32
Thalassophryne																
amazonica	10			3	7											
megalops	42*		2	36*												
maculosa	77*		7	44	15*	2										
nattereri	25*				3	17*	4									
punctata	3*					3*										
montevidensis	3		1	2												
Daector																
reticulata		40*					1	–	–	4	30*	1	1			
gerringi		1*											1*			
dowi		144*											1	11	87*	18

USNM 200404 (2, 40.0–45.3), OREGON 5739, 9°43′ N, 79°20′ W, 52 fms, 19 Oct. 1965.

Colombia. USNM 37669 (1, 53.9), holotype and USNM 197643 (1, 41.7), paratype of *T. megalops*, Gulf of Darien, ALBATROSS 2142, 9°31′ N, 76°20′ W, 42 fms, 23 March 1894.

Thalassophryne maculosa Günther
Fig. 6

Thalassophryne maculosa Günther, 1861:175 (original description; Puerto Cabello); Günther, 1869:436–437 (description after Günther, 1861), pl. 68, figs. 1–2 (holotype of *T. maculosa*). Meek and Hall, 1885:53–54 (after Günther). Jordan and Evermann, 1898:2324 (synonymy; description after Günther). Gill, 1907:403 (listed). Ogilby, 1908:55 (listed). Bean and Weed, 1910: not description pp. 519–521 but only pl. 33 (after Günther, 1869, pl. 68, figs. 1–2). Metzelaar, 1919:160 (specimen from Aruba). Rendahl, 1940:3 (comparison with *T. gerringi*). Cervigón M., 1966:862 (description, biology, Venezuela).

Thalassophryne maculatus [sic], Starks 1913: 72 (after Günther; compared with *T. branneri*).

Thalassophryne quadrizonatus Eigenmann, 1922:217 (original description; Río Truando, Colombia), pl. 29, fig. 5. Rendahl, 1940:3 (comparison with *T. gerringi*). Fowler, 1944:473 (listed).

Thalassophryne wehekindi Fowler, 1931:404–405 (original description; Trinidad), fig. 5. Cervigón M., 1965:70 (Venezuela; common name "sapo cano").

Thalassophryne megalops Caldwell and Caldwell (*non* Bean and Weed, 1910), 1964:41, figs. 1–3 (Colombia and Aruba).

Types.—*Thalassophryne maculosa* Günther, 1861. Holotype BMNH 1847.5.14.35 (94.0 mm), "Puerto Cabello, South America," purchased from Mr. Brandt. Dorsal rays II-19; anal 18; pectoral 15–15; vertebrae 7 + 21 but one vertebra apparently represents a fusion of two vertebrae so the count should probably be 7 + 22. The holotype is faded but

TABLE 2. NUMBER OF SECOND DORSAL RAYS IN SPECIES OF THALASSOPHRYNINAE. (* Indicates counts of types.)

Species	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33
Thalassophryne																	
amazonica			1	5	3												
megalops	2	33*	6														
maculosa	11	52*	15	1													
nattereri			3	19*	3												
punctata				2*	1												
montevidensis		4*	9														
Daector																	
reticulata						1	–	–	4	36*	2	1					
gerringi												1*					
dowi													1	19	31*	23	1

TABLE 3. NUMBER OF ANAL RAYS IN SPECIES OF THALASSOPHRYNINAE. (* Indicates counts of types.)

Species	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
Thalassophryne															
amazonica			4	6											
megalops	5	31*	5												
maculosa	9	54	13*	3											
nattereri			3	19*	3										
punctata				3*											
montevidensis		8	5*												
Daector															
reticulata						1	–	–	3	37*	2	1			
gerringi												1*			
dowi													9	94	42*

spots are still visible between the pectoral rays. The diameter of the eye is 4.3 mm.

The type-locality of *T. maculosa* is Puerto Cabello, Venezuela but has erroneously been considered to be the Puerto Cabello on the Guatemala–Honduras border. In his original description, Günther (1861) merely noted "Puerto Cabello." In his 1869 account of Central American fishes, Günther again gave the locality for *T. maculosa* as Puerto Cabello and also included a map (plate 63) which showed such a locality on the border of Guatemala and Honduras. Most subsequent authors have used the name *maculosa* for the species of *Thalassophryne* found off the coast of South America from British Guiana to Brazil. In reporting on a specimen of *T. maculosa* from Aruba, Metzelaar (1919:160) noted the type-locality of the species as "Puerto Cabello, Venezuela." Dr. Greenwood has informed me that the British Museum register reads, "Puerto Cabello, South America" for the type. The holotype of *T. maculosa* has the characters of the Colombia–Venezuela species (spots between the pectoral rays, no light distal margin to second dorsal, anal, pectoral, and caudal fins, and a large eye) not the British Guiana–Brazil species (here called *nattereri*).

Thalassophryne quadrizonata Eigenmann, 1922. Holotype Carnegie Museum 3921 A (35 mm), Río Truanda, Colombia. This specimen is no longer at the Carnegie Museum (Dr. M. Graham Netting, pers. comm.) and apparently never arrived in Chicago where the Carnegie fish collections were transferred. It is not in the Field Museum collection nor was an FMNH number entered in the Carnegie Museum register as was done for most of the Carnegie fishes. The figure in Eigenmann (1922, pl. 29, fig. 5) leaves little doubt as to the identity of this species.

Thalassophryne wehekindi Fowler, 1931.

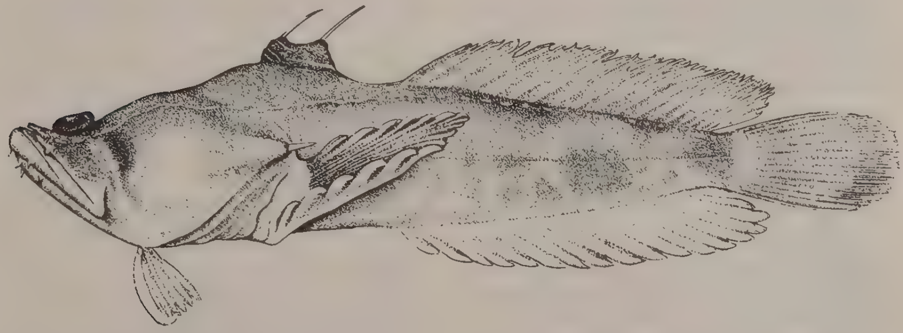

Fig. 5. *Thalassophryne megalops* Bean and Weed. USNM 187946, 61.5 mm SL, Atlantic coast of Panama, 75 fms.

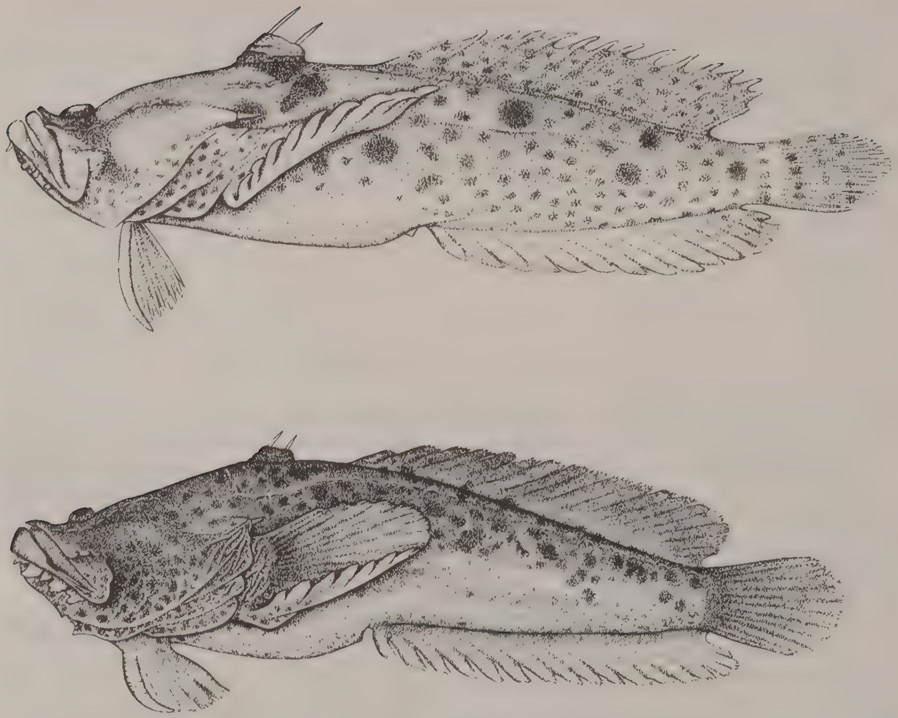

Fig. 6. *Thalassophryne maculosa* Günther. Upper: USNM 199485, 72.9 mm SL, Cariaco Trench off Venezuela, 40 fms. Lower: USNM uncat., 134 mm SL, Golfo de Cariaco, Venezuela.

Holotype ANSP 53315 (53.0 mm), Gasparee Island off Trinidad, 26 June 1950. Dorsal rays II-18; anal 17; pectoral 15; vertebrae 7 + 19.

Diagnosis.—A large species of *Thalassophryne* that shows great variation in the number and shape of the spots and blotches that cover the body and the pectoral fins. Counts for the large number of specimens available overlap most of the species of *Thalassophryne*: second dorsal rays 17–20, usually 18; anal 16–19, usually 17; pectoral 14–16, usually 15; caudal vertebrae 19–22, usually 20. The eye diameter of *T. maculosa* is larger than that of *T. nattereri* (Fig. 7) and the other species of Thalassophryninae except *T. megalops* (Table 7).

Small specimens tend to be light with small to medium dark spots and blotches (Fig. 6, upper, and Fowler, 1931, fig. 5). Large specimens tend to have a darker ground color with smaller spots which do not stand out as well as in smaller specimens (Fig. 6, lower).

Remarks.—According to Dr. Cervigón (pers. comm.), the fishermen of Isla Margarita believe that *Thalassophryne* deposits its eggs when its spines puncture someone's flesh, and that the eggs cause the resulting pain which may be moderately severe. The natives employ a number of popular remedies such as hot lemon, chewed tobacco, garlic, etc. *T. maculosa,* although edible, is not usually eaten; it is used for food in only a few localities. (See also Cervigón M., 1966).

T. maculosa is common on sandy beaches on the leeward side of Isla Cubagua and the south side of Isla Margarita (Dr. Cervigón, pers. comm.). Dr. Randall has taken specimens buried in sand with only the eyes showing. Numerous specimens of *T. maculosa* were taken with seines by Dr. William A. Lund near Cumaná, Venezuela. The R/V OREGON has collected *T. maculosa* with shrimp trawls at depths of 35–100 fms.

Table 4. Correlation Between Number of Caudal Vertebrae and Second Dorsal Rays in *Thalassophryne maculosa*.

Second Dorsal Rays	Caudal Vertebrae 19	20	21	22	N
17	4	6			10
18		55	8		63
19		1	26	9	36
20				5	5
N	4	62	34	14	114

Table 5. Correlation Between Number of Caudal Vertebrae and Second Dorsal Rays in *Daector dowi*.

Second Dorsal Rays	Caudal Vertebrae 29	30	31	32	N
29	1				1
30		11	4	1	16
31		1	79		80
32			2	16	18
33				1	1
N	1	12	85	18	116

Range.—The northern coast of South America off Colombia and Venezuela including the islands of Aruba, Curaçao, Margarita, Cubagua, Trinidad, and Tobago but not extending into the Antilles proper (Fig. 4).

Material examined.—Colombia. USNM 200405 (1, 72.7), Oregon 5727, 8°47′ N, 77°09′ W, 43 fms, 17 Oct. 1965. USNM 199524 (9, 60.3–81.2), Oregon 4899, 8°50.5′ N, 76°53.5′ W, 37–40 fms, 27 May 1964. TABL uncat. (5, 60.9–74.0), Oregon 4898, 8°53.8′ N, 76°51.6′ W, 100 fms, 27 May 1964. USNM 199527 (1, 59), Oregon 4884, 9°59.9′ N, 75°55.2′ W, 55–60 fms, 25 May 1964. CAS 15317 (1, 70.1), Cartegena?, Eigenmann. LACM 20056 (1, 61.6), Allan Hancock Foundation 2764, Velereo III sta. A-15-39, 2 miles off Bahia Honda, 12°24′ N, 71°47′ W, 9 fms, 8 April 1939. USNM 200406 (1, 89.1), Oregon 5704, 11°56′ N, 72°32′ W, 15 fms, 12 Oct. 1965. UF 11622 (2, 77.6–90.1), Oregon 4919, 12°04′ N, 72°18′ W, 10 fms, 1 June 1964. USNM 200407 (1, 83.3), Oregon 5695, 12°04′ N, 72°15′ W, 15 fms, 12 Oct. 1965.

Gulf of Venezuela. UF 11619 (27, 67.3–97.0), Oregon 4391, 12°33′ N, 71°09′ W, 40 fms, 25 Sept. 1963. TABL uncat. (1, 42.5), Oregon 4392, 12°32′ N, 71°05′ W, 40 fms, 25 Sept. 1963. TABL uncat. (1, 85.0), Oregon 4393, 12°32′ N, 71°04′ W, 40 fms, 25 Sept. 1963. USNM 199494 (1, 110), Punto Fijo, Paraguaná Peninsula, 29 Jan. 1965, J. E. Randall.

Aruba. RNH 23523 (1, 60.4), "Piez Arena," 5 Sept. 1955. LACM 20055 (4, 18.9–73.1), Allan Hancock Foundation 2765, Sta. A-18-39, 8 miles SW San Nicolaas Is.

Curaçao. RNH 23183 (2, 96.5–103.5), Caracas Bay, 20 April 1955.

Venezuela. USNM 199485 (3, 33.5–72.9), NE part Cariaco Trench, Atlantis, 40 fms, 3 Nov. 1957. MBUCU-V-1940 (2, 66.2–88.8), Chichiriviche Bay, 13 km W La Guaira, Distrito Federal, 5 Jan. 1964. ANSP 102065 (2, 40.5–60.3), Golfo de Cariaco, Quetepe, 23 Dec. 1961, W. A. Lund 200. USNM 200557 (10, 46.0–111) and BMNH unreg. (1, 100), Bahia de Mochima, 4 March 1962, W. A. Lund 209. ANSP 102066 (1, 87.0), Bahia de Mochima, 0.5 mile W Mochima, 4 March 1962, W. A. Lund 210. ANSP 103618 (2, 34.6–85.0), Golfo de Cariaco, 1.5 miles off Cariaco, 6–7 March 1962, W. A. Lund 214. ANSP 102063 (1, 121), Golfo de Cariaco, Mariquetar, 10 March 1962, W. A. Lund 215. USNM 200558 (22, 25.6–140), FMNH 66831 (1, 63.6), MCZ 45046 (2, 37.0–74.8), Golfo de Santa Fe, 15 March 1962, W. A. Lund 217. ANSP 103619 (5, 39.8–124), Araya Peninsula, Punta Homo, 17 March 1962, W. A. Lund 219. USNM 199493 (1, 120), Isla de Cubagua, off Isla Margarita, May 1963, F. Cervigón. USNM 199495 (2, 30.8–83.3) and UPR 2474 (2, 87–94), Isla de Cubagua, 23 Jan. 1965, J. E. Randall. UPR 2481 (1, 79), Isla de Cubagua, 19 Jan. 1965, J. E. Randall. USNM 199492 (1, 150), Las Galeritas, I. Margarita, 21 Aug. 1956, F. Cervigón. USNM 199491 (1, 89), I. Margarita, 1949–1950. USNM uncat. (3, 88.1–93.1), Isla Blanca, 15 July 1965, F. Cervigón. UF 11621 (1, 66.3), Oregon 4481, 11°14′ N, 64°13′ W, 30 fms, 22 Oct. 1963. USNM 199528 (1, 55.5), Oregon 5033, 11°06′ N, 62°40′ W, 30 fms, 23 Sept. 1964.

Trinidad. ANSP 53315 (1, 53.0), Gasparee Is., 26 June 1950, L. Wehekind, holotype of *T. wehekindi*. UPR 1158 (1, 51.0), Los Cuevos Bay, 5 Jan. 1962, J. E. Randall. UPR 1805 (7, 47.7–98.2), Chupara Pt., 7 May 1964, J. E. Randall.

Tobago. TABL uncat. (2, 51.2–58.3), Oregon 5023, 11°14′ N, 60°51′ W, 38 fms, 21 Sept. 1964. USNM 199526 (3, 51–63), Oregon 5025, 11°08′ N, 60°58′ W, 40–48 fms, 21 Sept. 1964. USNM 199525 (2, 76–90), Oregon 5030, 11°09′ N, 60°55′ W, 35–37 fms, 22 Sept. 1964.

Thalassophryne nattereri Steindachner

Fig. 8

Thalassophryne nattereri Steindachner, 1876: 163–165 (original description; Pará, Brazil). Meek and Hall, 1885:53–54 (after Steindachner). Ogilby, 1908:55 (listed). Miranda-Ribeiro, 1915:629–630 (after Steindachner).

Thalassophryne maculosa Pellegrin (*non* Günther, 1861), 1908:586 (in part; Ilet Le Père, French Guiana; poison apparatus). Bean and Weed, 1910:519–521 (description; *T. nattereri* considered a synonym of *T. maculosa*), not pl. 33 (type of *T. maculosa*, after Günther). Eigenmann, 1922:217 (comparison with *T. quadrizonatus*). Jordan, Evermann, and Clark, 1930:488 (listed). Puyo, 1936:229 (listed from French

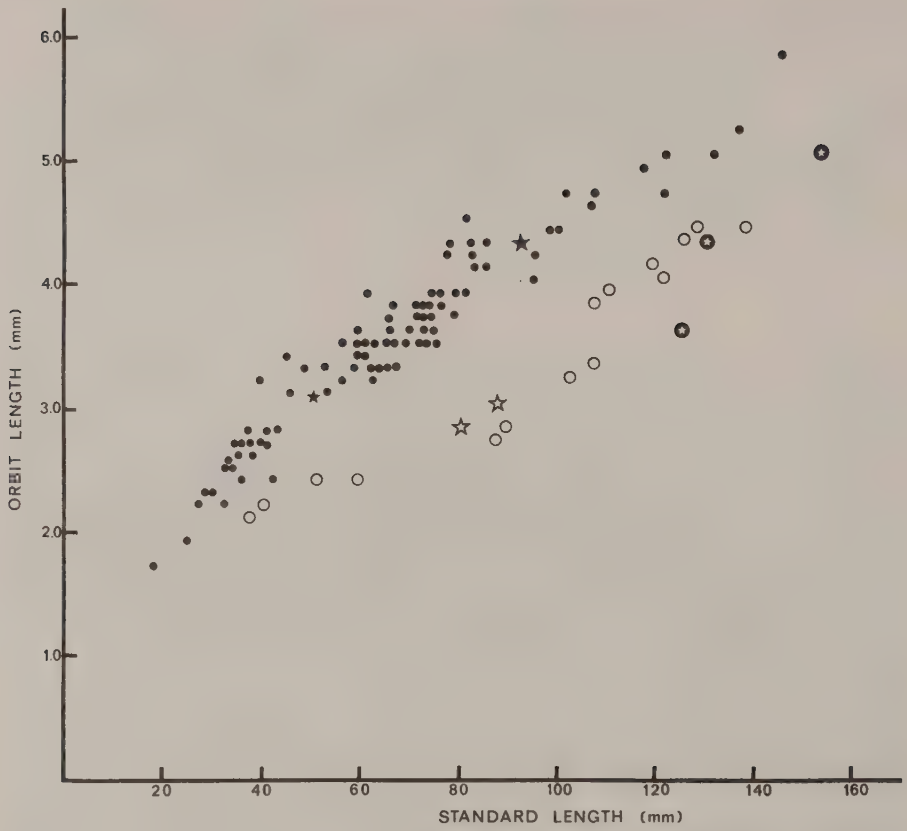

Fig. 7. Orbit diameter in *Thalassophryne maculosa* (solid symbols), *T. nattereri* (open symbols), and *T. punctata* (circled stars). Stars represent type specimens: large solid star — *T. maculosa*, small solid star — *T. wehekindi*, open stars — *T. nattereri*, circled stars — *T. punctata*.

Guiana). Puyo, 1949:253–254 (description, ecology, French Guiana).

Thalassophryne branneri Starks, 1913:72–73 (original description; common name "moreiatim"; Natal, Brazil); pl. 13. Miranda-Ribeiro, 1915:631 (description; San Salvador, Brazil). Fowler, 1941:180 (reference to Starks and Miranda-Ribeiro). Lowe, 1962:696 (British Guiana in less than 10 fms over soft brown mud).

Types.—*Thalassophryne nattereri* Steindachner, 1876. Lectotype MCZ 12726 (81.0 mm), Pará, Brazil, herein selected. Dorsal II-20, anal 19; pectoral 16–14; vertebrae 7 + 22 = 29; orbit diameter 2.8 mm. Paralectotypes MCZ 4631 (2, 65.7–74), Pará, Brazil, badly dried, and NMV uncat. (1, 88.0).

Thalassophryne branneri Starks 1913. Holotype SU 2223 (149 mm), Natal, Brazil. Dorsal rays II-20; anal 19; pectoral 16–16; vertebrae 7 + 22 = 29.

Diagnosis.—A large species of *Thalassophryne* with pale distal margins to the dark, unspotted dorsal, anal, pectoral, and caudal fins (Fig. 8). Counts are higher than the other species of *Thalassophryne*, similar to *T. punctata*: second dorsal rays 19–21, usually 20; anal 18–20, usually 19; pectoral 15–17, usually 16; caudal vertebrae 21–23, usually 22. The diameter of the orbit is 31–54 thousandths of standard length, smaller than in *T. megalops* and *T. maculosa* (Fig. 7) and about the same size as in *T. montevidensis* (Table 7).

TABLE 6. NUMBER OF PECTORAL FIN GLANDS AND PECTORAL FIN RAYS IN SPECIES OF THALASSOPHRYNINAE. (* Indicates counts of types.)

Species	Pectoral Glands								Pectoral Rays					
	0	1	2	3	4	5	6	7	13	14	15	16	17	18
Thalassophryne														
amazonica	10									5	5			
megalops	42*								4	32*	6			
maculosa	81*									8	49*	21		
nattereri	25*										4	18*	3	
punctata	3*									1	1*	1		
montevidensis	14*										3	10*	1	
Daector														
reticulata							36*	8				14*	29	1
gerringi				1*							1*			
dowi				2	41*	75	22					57*	79	8

Remarks.—This species has been long confused with *T. maculosa* (see remarks under that species).

Range.—Tobago and the coast of South America from British Guiana east and south at least as far as San Salvador, Brazil.

Material examined.—Tobago. BMNH 1924.7.22.88–89 (2, 104.0–108.7), Guppy.

British Guiana. BMNH 1961.9.4.174 (1, 134), CAPE ST. MARY. BMNH unreg. (1, 123), CAPE ST. MARY 992, 6°40′ N, 57°22′ W, 4 Feb. 1959.

French Guiana. MNHN 03–40 (1, 109), Geay. MNHN 04–19 (1, 60.6), Geay.

Brazil. TABL uncat. (1, 41.2), OREGON 4207, 4°46′ N, 51°21′ W, 32 fms, 26 Feb. 1963. UMML 11535 (1, 121), OREGON 4209, 4°30′ N, 50°52′ W, 36 fms, 27 Feb. 1963. USNM 187975 (1, 52.3), OREGON 2078, 1°50′ N, 47°28′ W, 40 fms, 17 Nov. 1957. FMNH 66273 (1, 126), OREGON 4215, 0°27′ S, 47°09′ W, 12 fms, 8 March 1963. MCZ 12726 (1, 81.0) lectotype, MCZ 4631 (2, 65.7–74) and NMV uncat. (1, 88.0), paralectotypes of *T. nattereri*, Pará (Belém), Brazil. MCZ 12724 (2, 112–127), Curucá. FMNH 66275 (1, 101), OREGON 4232, 2°00′ S, 42°45′ W, 28 fms, 10 March 1963. USNM 200555 (1, 38.6), OREGON 4258, 3°04′ S, 39°09′ W, 16 fms, 13 March 1963. SU 2223 (1, 149), holotype of *T. branneri*, Natal, 1911. BMNH 1863.3.27.13 (1, 88.8), Bahia (Salvador), Wucherer. MNHN A 34-19 (2, 130–140), Bahia (Salvador), Brunet. MNRJ 1524 (1, 110), Salvador. MNRJ 2451 (1, 91). SU 34821 (1, 90.6).

Thalassophryne punctata Steindachner

Thalassophryne punctata Steindachner, 1876: 169–170 (original description; Bahia and Porto Seguro, Brazil). Meek and Hall, 1885:53–54 (after Steindachner). Ogilby, 1908:55 (listed). Bean and Weed, 1910: 518–519 (description; Brazil). Miranda-Ribeiro, 1915:628–629 (after Steindachner). Fowler, 1941: 180 (reference to Steindachner).

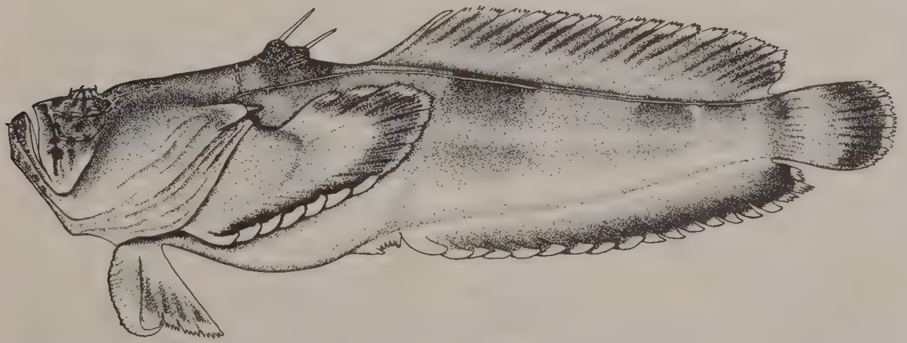

Fig. 8. *Thalassophryne nattereri* Steindachner. UMML 11535, 121 mm SL, off French Guiana-Brazil border, 36 fms.

TABLE 7. ORBIT DIAMETER AND INTERORBITAL DISTANCE IN SPECIES OF THALASSOPHRYNINAE (IN THOUSANDTHS OF STANDARD LENGTH).

Species	N (size in mm)	Orbit		Interorbit		$\frac{\text{Interorbit}}{\text{Orbit}}$	
		Range	$\bar{X}$	Range	$\bar{X}$	Range	$\bar{X}$
Thalassophryne							
amazonica	9 (32–93)	26–40	32.7	65–88	75.7	1.75–3.05	2.38
megalops	25 (36–62)	54–67	61.6	48–61	55.1	0.75–1.06	0.90
maculosa	112 (34–148)	37–78	53.6	40–71	57.4	0.58–1.87	1.10
nattereri	14 (39–140)	31–54	37.7	46–74	61.1	0.86–2.36	1.70
punctata	3 (127–158)	28–33	31.0	61–71	67.3	2.12–2.22	2.17
montevidensis	18 (88–151)	33–43	38.8	70–102	83.1	1.83–2.95	2.10
Daector							
reticulata	17 (30–252)	29–62	42.0	42–70	59.1	0.59–2.16	1.59
gerringi	1 (116)		20.7		59.5		2.88
dowi	39 (55–135)	18–28	22.5	43–63	51.1	1.73–2.76	2.29

Types.—Lectotype MCZ 4632 (132 mm), Brazil, Porto Seguro, Thayer Expedition, herein selected. Dorsal rays II-20; anal 19; pectoral 15–14; vertebrae 7 + 22 = 29; diameter of orbit 4.3 mm; body and fins tan with very fine dark spots. Paralectotypes? NMV uncat. (158 mm) and MCZ 12725 (127 mm), Brazil, Bahia (Salvador). MCZ 4632 is labeled "type" and MCZ 12725 "cotype." Bean and Weed (1910) considered MCZ 4632 as a cotype and MCZ 12725 as non-type material. NMV uncat. is not labeled as a type but is probably part of the type series except that the label is dated 1876. I have selected MCZ 4632 as lectotype because it was most likely one of the type series, and because it is in the best condition of the three specimens.

Diagnosis.—A medium-sized species of *Thalassophryne* close to, and perhaps identical with, *T. nattereri.* The body of *T. punctata* has much smaller and rounder spots on a lighter background than *T. nattereri* and appears to lack the light distal margins on the second dorsal, anal, pectoral, and caudal fins characteristic of *T. nattereri.* In all meristic characters the three specimens of *T. punctata* agree with *T. nattereri*: second dorsal rays 20–21; anal 19; pectoral 14–16; caudal vertebrae 22. In orbit diameter, which distinguishes the larger-eyed *T. maculosa* from the smaller-eyed *T. nattereri,* the three specimens of *T. punctata* are similar to *T. nattereri* (Fig. 7).

Range and material examined.—Limited to the middle of the Brazilian coast line from Salvador to Porto Seguro on the southern end of the range of *T. nattereri* (Fig. 4). Only three specimens (discussed under types) known.

Thalassophryne montevidensis Berg
Fig. 9

Thalassophryne montevidensis Berg, 1893: 6–7 (original description; Montevideo, Uruguay), pl. 2.

Thalassothia montevidensis, Berg, 1895:67 (new genus *Thalassothia* described for *Thalassophryne montevidensis*), pl. 1. Ogilby, 1908:55 (listed). Bean and Weed, 1910:525–526 (after Berg). Devincenzi, 1924:258–259 (the holotype of *T. montevidensis* the only specimen known). Pozzi and Bordale, 1935:177 (listed from Argentina). Devincenzi and Legrand, 1940, pl. 39. Soriano Señorans, 1958:14 (a valid genus and species; measurements of "tipo" and "cotipo"). Ringulet and Arámburu, 1960:85 (listed; reference to Buen, 1950).

Thalassophryne platensis Devincenzi, 1924: 260–262 (original description, Punta Carretas, Río de La Plata; common name "bagre sapo ponzoñoso"). Buen, 1950:126 (reference to Devincenzi). Soriano Señorans, 1958:12–13 (valid species), drawing of holotype. Ringulet and Arámburu, 1960:85 (listed; Argentina, Uruguay).

Thalassophryne maculosa, Devincenzi (*non* Günther, 1861), 1924:259–260 (three specimens from Río de La Plata). Devincenzi and Legrand, 1940, pl. 39. Buen, 1950:126 (reference to Berg and Devincenzi; *Thalassothia montevidensis* considered as possible synonym). Ringulet and Arámburu, 1960: 85 (listed; common names "bagre sapo pon-

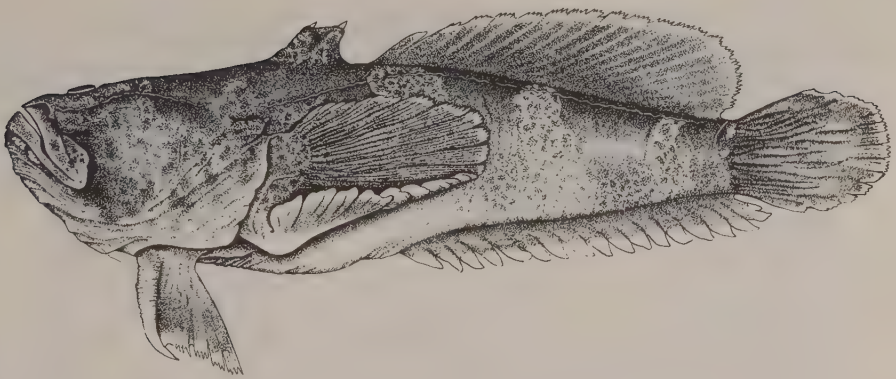

Fig. 9. *Thalassophryne montevidensis* Berg. USNM 200350, ♀, 102 mm SL, Uruguay, Río de La Plata.

zoñoso, pez sapo ponzoñoso"; Argentina, Uruguay).

Types.—*Thalassophryne montevidensis* Berg, 1893. Holotype MNM 37 (♀, 129.2), Uruguay, Río de La Plata, Montevideo, Punta Carretas, Nov. 1891. Dorsal rays II-18; anal 17; pectoral 16–16; diameter of orbit 5.2 mm; first two rays of second dorsal fin broken.

Thalassophryne platensis Devincenzi, 1924. Holotype MNM 196 (♂, 150.7), Uruguay, Río de La Plata, Montevideo, Punta Carretas, 25 Jan. 1921, C. Vivani. Dorsal rays II-19; anal 18; pectoral 15; diameter of orbit 5.2 mm.

Diagnosis.—A large dark-colored species of *Thalassophryne* with four tan dorsal saddles under the second dorsal fin and with pale distal margins to the second dorsal anal, pectoral, and caudal fins (Fig. 9) as in *T. nattereri.* In most counts *T. montevidensis* is similar to *T. maculosa*: second dorsal rays 18–19; anal 17–18; caudal vertebrae 19–20. In number of pectoral rays *T. montevidensis* is most similar to *T. nattereri* (15–17 rays, usually 16). *T. montevidensis* has a fairly small eye (33–43 thousandths of standard length) similar to *T. nattereri* (Table 7). However, *T. montevidensis* has a much larger interorbital distance (70–102 thousandths of standard length compared to 46–74 in *T. nattereri*).

Remarks.—The species *montevidensis* (Berg, 1893) and the nominal genus *Thalassothia* (Berg, 1895) were based on the holotype having four dorsal spines. Devincenzi (1924) and Soriano Señorans (1958) both agreed with Berg on this character. I examined the type and found that the supposed two spines in the second dorsal fin are the first two soft rays broken off short so that only about a third of each ray remains. The species, however, is valid.

Range.—*T. montevidensis* appears to be limited to the north shore of Río de La Plata from Montevideo to Punta del Este (Fig. 4).

Material examined. Uruguay, Río de La Plata. MNM 37 (1, 129), Punta Carretas, Nov. 1891, holotype of *Thalassophryne montevidensis.* MACN 5267 (1, 130), Montevideo, 30 March 1896, originally no. 3073, specimen believed by Soriano Señorans (1958) to be a cotype of *T. montevidensis.* MACN 1931 (1, 103), Maldonado. MNM 196 (1, 151), Punta Carretas, 25 Jan. 1921, holotype of *T. platensis.* MNM 415 (1, 143), Punta del Este, 1936. MNM 481 (1, 97.5), Isla de Flores, 25 June 1940. MNM 635 (10, 93.9–133), and USNM 200350 (3, 88.4–122), Isla Gorriti, Bahia de Maldonado, 1954.

Daector Jordan and Evermann

Daector Jordan and Evermann, 1898:2325 (original description, type-species *Thalassophryne dowi* Jordan and Gilbert, 1887, by original designation).

Daector differs from *Thalassophryne* primarily in having discrete glands between the bases of the upper 3–7 rays of the pectoral fin (Fig. 1), as in *Opsanus* (Wallace, 1893). These glands open through pores on the inner surface of the fin. The glands have not been reported previously in this subfamily and their function is unknown. The species of *Daector* have a stripe running the length of either the second dorsal fin (in *dowi*), the

Table 8. Morphometric Comparison of a Specimen Tentatively Referred to *Daector reticulata* with Smaller and Larger Specimens of *D. reticulata* in Per Cent of Standard Length.

	D. reticulata		Variant	*D. reticulata*	
Cat. No.	USNM 81697	SU 22287	SU 14949	SU 22287	SU 22287
Standard length (mm)	52.7	53.8	80.1	167	193
Head length	31.3	32.0	36.0	30.5	32.0
Head width	28.8	30.1	34.5	32.2	30.1
Snout–1st dorsal	29.2	26.2	29.6	28.2	29.7
Snout–2nd dorsal	39.3	37.7	45.8	44.6	44.2
2nd dorsal base	55.6	56.1	49.2	52.4	57.5
Snout–anal	42.5	42.0	52.7	45.6	45.0
Anal base	55.6	56.9	52.8	54.3	54.9
Snout–pectoral	30.6	29.9	36.7	30.7	31.5
Pectoral length	27.5	29.7	27.2	25.0	25.2
Snout–pelvic	18.8	19.7	21.7	19.5	19.5
Pelvic length	18.0	17.1	20.0	17.5	16.6

anal fin (in *reticulata*), or both (in *gerringi*). No species of *Thalassophryne* has a similar stripe in either fin. *Daector* also differs from *Thalassophryne* in having 8 instead of 7 precaudal vertebrae and more caudal vertebrae (23–32 instead of 19–23), second dorsal (22–33 *vs.* 17–21), and anal rays (21–30 *vs.* 16–20). In *Daector* the number of second dorsal rays is either equal to the number of caudal vertebrae (*dowi*) or one less, instead of two less as in *Thalassophryne* (compare Tables 4 and 5). The three Pacific species of venomous toadfishes belong to *Daector*: *reticulata* Günther, *gerringi* Rendahl, and *dowi* Jordan and Gilbert. They are better differentiated from each other meristically and in color pattern than are the western Atlantic species.

Daector reticulata (Günther)
Fig. 10

Thalassophryne reticulata Günther, 1864a:150 (original description; Pacific coast, Panama). Günther, 1864b:155–157, figs. 1, 2 (poison apparatus). Günther, 1869:437–439 (description; effect of poison after Dow, 1865), figs. 1, 2 (poison organ), pl. 68, fig. 2 (holotype). Günther, 1880:191–192, fig. 100 (poison apparatus after Günther, 1869), p. 468, fig. 208. Jordan and Gilbert, 1883:626 (Panama). Meek and Hall, 1885: 54–55 (after Günther and Jordan and Gilbert). Savtschenko, 1887:39 and pl. 10, fig. 1 (after Günther). Jordan and Evermann, 1898:2325 (synonymy; description; Panama). Gilbert and Starks, 1904:186–187 (description; Panama). Gill, 1907:403 (after Günther, fig. 115 mislabeled as *T. maculosa*). Ogilby, 1908:55 (listed). Bean and Weed, 1910:522–523 (description; Panama), fig. 7 (teeth). Phisalix, 1922:511–512, fig. 211, p. 536 (poison apparatus after Günther, 1869). Meek and Hildebrand, 1928:920 (description; Balboa and Panama City). Jordan, Evermann, and Clark, 1930: 488 (listed). Rendahl, 1940:3 (comparison with *T. gerringi*). Fowler, 1944:235 (synonymy; Playa Muerto, Panama).

Thalassophryne sp., Dow, 1865:677 (natives familiar with presence of spines and emission of poison).

Type.—BMNH 1864.1.26.342 (225 mm), Pacific coast of Panama, Salvin. Dorsal rays II-26; anal 25; pectoral 16–16; vertebrae 8 + 27 = 35.

Diagnosis.—*D. reticulata* is the largest species of the subfamily, reaching a standard length of 270 mm. It has a very characteristic reticulated body pattern, totally unlike any of the other species (Fig. 10). It has the lowest number of second dorsal (25–28, usually 26) and anal rays (24–27, usually 25) and caudal vertebrae (26–29, usually 27) of any of the genus *Daector* but more than any of the genus *Thalassophryne.* In number of pectoral rays (16–18, usually 17) it is similar to *D. dowi* but it has more (6 or 7) pectoral fin glands.

Remarks.—*D. reticulata* is the best known species in the subfamily because Günther's description (1864b) of the venom apparatus and Dow's 1865 account of poisoning of natives in Panama have been copied by many subsequent authors.

One small specimen (SU 14949, 80.4 mm) is

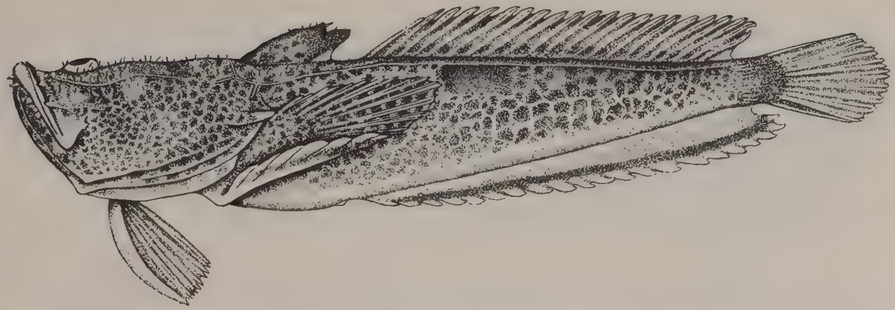

Fig. 10. *Daector reticulata* (Günther). Variant specimen, SU 14949, 80.4 mm SL, Costa Rica, Golfo de Nicoya.

tentatively referred to *D. reticulata* although it may prove to represent an undescribed species. This specimen is apparently from tide pools on Negritos Island in the Gulf of Nicoya, Costa Rica, although there seems to be some doubt as to the accuracy of the locality. It has the same color pattern and cephalic filaments (Figs. 3, 10) as *D. reticulata* but differs in the following three counts: second dorsal rays (22 *vs.* 25–27); anal rays (21 *vs.* 24–26); and caudal vertebrae (23 *vs.* 26–28). It has the same number of pectoral rays (16) and pectoral glands (6) as *D. reticulata*. This specimen shows some morphometric differences but I hesitate to place much confidence in them because comparisons were based on specimens 30 mm smaller (52.7 and 53.8 mm SL) and 80 mm larger (167 and 193 mm SL) than the variant. With this limitation in mind, it appears (Table 8) that the variant specimen has a slightly longer and wider head, shorter second dorsal and anal fin bases, shorter snout-to-anal distance, longer pectoral and pelvic fins, and a greater snout-to-pelvic distance. Many of these differences are attributable to the shorter body (at least three vertebrae shorter).

Range.–Except for the variant specimen from the Golfo de Nicoya, Costa Rica, all known specimens are from the Gulf of Panama (Fig. 4), so detailed locality data are not given in the list of material examined.

Material examined.–Costa Rica: SU 14949 (1, 80.4), Golfo de Nicoya, Isla Negritos, 13 Feb. 1947, M. B. Schaefer.

Panama: BMNH 1864.1.26.342 (1, 225), Pacific coast of Panama, holotype of *D. reticulata*. BMNH 1866.1.14.11–12 (2, 251–270); 1903.5.15. 193–4 (2, 203–264). USNM 81698 (2, 187–209); 81699 (1, 200); 81696 (1, 38.5); 81697 (1, 52.7); 81700 (2, 233–252); 81701 (1, 226); 50409 (1, 244); 81970 (1, 29.5); 144880 (2, 30.2–36.7). ANSP 70346 (1, 257). MCZ 41806 (3, 143–255). UBC 60-127 (1, 214); 59-668 (1, 185); 59-685 (4, 106–202). SIO 64-353 (1, 152). SU 22287 (4, 53.8–218); 57004 (1, 36.3); 57003 (1, 24.5). UCLA W53-310 (1, 163); W53-273 (1, 172); W58-305 (2, 150–220); W58-278 (5, 169–223).

Daector gerringi (Rendahl)
Fig. 11

Thalassophryne gerringi Rendahl, 1940:1–3 (original description); Rio San Juan, Colombia, fig. 1.

Holotype.–NRS 10651 (116.0 mm), Colombia, Choco district, Cabeceras coast, Rio San Juan, 1939. Dorsal rays II-28; anal 27; pectoral 15–15; pectoral fin glands 3–2; vertebrae $8 + 29 = 37$.

Diagnosis.–A light-colored, medium-sized species of *Daector*, with four prominent dark dorsal saddles and with the second dorsal, anal, and caudal fins light basally, dark medially, and light distally. In counts of second dorsal and anal rays, and caudal vertebrae, *D. gerringi* is intermediate between *D. dowi* and *D. reticulata* although overlapping one specimen of the latter species. *D. gerringi* has fewer (15) pectoral rays than the other two Pacific members of the genus.

Range and material examined.–The holotype and only known specimen from Colombia (Fig. 4).

Daector dowi (Jordan and Gilbert)
Fig. 12

Thalassophryne dowi Jordan and Gilbert, 1887:388 (original description; Puntarenas, Costa Rica). Jordan, 1896:231, pl. 38 (Panama). Gilbert and Starks, 1904:187–188 (description, Panama; *Daector* a synonym

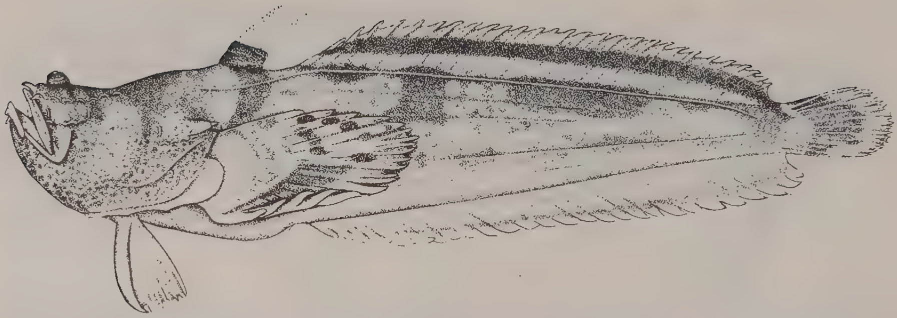

Fig. 11. *Daector gerringi* (Rendahl). Holotype, NRS 10561, 116 mm SL, Colombia, Choco District.

of *Thalassophryne*). Gill, 1907:403 (listed). Bean and Weed, 1910:514–517 (description), pl. 31 (after Jordan, 1896). Meek and Hildebrand, 1928:920–921 (description; Chame Point and Balboa, Panama). Jordan, Evermann, and Clark, 1930:488 (listed; *Daector* a subgenus of *Thalassophryne*). Rendahl, 1940:3 (comparison with *T. gerringi*). Fowler, 1944:525 (listed). Hildebrand, 1946:498 (comparison with *T. depressa*).

Daector dowi, Jordan and Evermann, 1898: 2325–2326 (*T. dowi* the type-species of *Daector*; synonymy; description). Ogilby, 1908:54 (listed).

Thalassophryne depressa Hildebrand, 1946: 497–499 (original description; Puerto Pizarro, Gulf of Guayaquil, Peru), fig. 95. Chirichigno F., 1963:80–81 (Peru), fig. 72.

Types.—*Thalassophryne dowi* Jordan and Gilbert, 1887. Holotype USNM 39085 (1, 82.1), Costa Rica, Puntarenas. Dorsal rays II-31; anal 30; pectoral 16–16; pectoral fin glands 4–4; vertebrae 8 + 31 = 39.

Thalassophryne depressa Hildebrand, 1946. Holotype USNM 128235 (1, 73.8), Peru, Gulf of Guayaquil, Puerto Pizarro, 10 May 1941, M. J. Lobell. Dorsal rays II-30; anal 28; pectoral 16–16; pectoral fin glands 4–3; vertebrae 8 + 30 = 38.

Diagnosis.—A slim medium-sized species of *Daector* with a prominent light stripe along the lateral line, the second dorsal fin base pale with a distal dark margin, and an unpigmented anal fin (Fig. 12). The last dorsal and anal rays are joined to the caudal fin but the three fins are not completely confluent as in *T. amazonica*. *D. dowi* has the highest number of second dorsal (29–33, usually 31) and anal rays (28–30, usually 29), and caudal vertebrae (29–32, usually 31) in the subfamily. It has the same number of pectoral rays (16–18, usually 17) as *D. reticulata* but fewer pectoral glands (3–6, usually 5, *vs.* 6 or 7), Table 6. *D. dowi* and *D. gerringi* have much smaller eyes than *D. reticulata* (12–28 thousandths of standard length compared to 29–62, Table 7).

Range.—*D. dowi* is the most widely distributed of the Pacific species, ranging from Puntarenas, Costa Rica (holotype) to the Gulf of Guayaquil, Peru (Fig. 4).

Material examined: Costa Rica: USNM 39085 (1, 82), Puntarenas, holotype of *T. dowi*.

Panama: USNM 41430 (1, 110); 41232 (2, 91–107); 82236 (3, 101–135); 81694-5 (3, 113–122); 188844 (11, 74–112). UBC 59-670 (4, 65–132); 59-664 (4, 93–104); 59-686 (2, 105–113); 59-685 (5, 83–113); 60-110 (3, 119–123); 59-665 (3, 44–120); 59-668 (3, 91–133). CU 2100 (1, 96). SU 6875 (1, 131); 410 (2, 55–120); 53113 (2, 115–119). UCLA 53-310 (3, 96–123); 53-273 (4, 82–138); 58-305 (32, 43–125). CAS 58-304 (14, 88–118). SIO 59-349-60 A (1, 95); 64-352 (1, 83); 64-354 (3, 42–62); 64-355 (1, 64); 64-356 (3, 58–67); 64-357 (1, 49); 64-358 (1, 45); 64-359 (2, 40–42); 64-360 (2, 52–66); 64-361 (1, 51); 64-362 (1, 53); 64-363 (1, 38); 64-364 (2, 67–84); 64-365 (2, 102–114); 64-366 (1, 120); 64-367 (1, 51); 64-368 (4, 43–64); 64-369 (2, 47–49); 64-370 (1, 66); 64-371 (4, 49–70). FMNH 62736 (2, 113–125).

Colombia: SIO 64-351 (1, 135), SE of Gorgona Is., off Boca Timbique, 6 June 1954.

Peru: USNM 128235 (1, 74), Gulf of Guayaquil, Puerto Pizarro, 10 May 1941, holotype of *T. depressa*. IMARPE 177 (1, 101), Puerto Pizarro–Punta Mal Pelo, Nov. 1954; 385 (1, 127), Puerto Pizarro, December 1959; 603 (1, 110), Estero Lagarto, Puerto Pizarro, December 1955.

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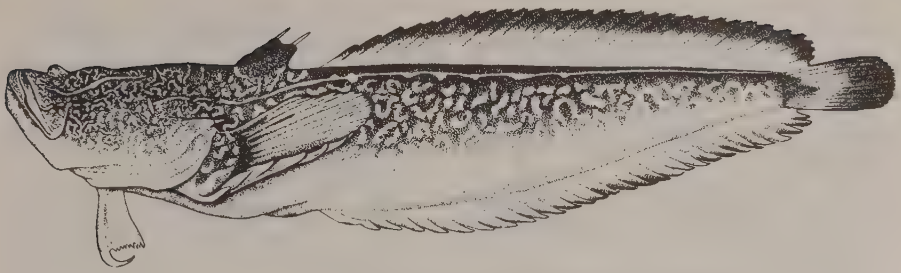

Fig. 12. *Daector dowi* (Jordan and Gilbert). SU 53113, 119 mm SL, Panama.

mation on its biology. Dr. James A. Peters (USNM) kindly arranged for the loan of eight specimens of *T. amazonica* through Dr. Gustavo Orcés Villagomez (EPN). Dr. P. H. Greenwood (BMNH) answered my numerous letters regarding the holotype of *T. maculosa.* Dr. Miguel Klappenbach (MNM) donated three specimens of *T. montevidensis* to the U. S. National Museum. Srta. Norma Chirichigno (IMARPE) sent me Peruvian specimens of *D. dowi* and contacted Felipe Ancieta (Universidad Nacional de Trujillo, Peru) so that I could examine two specimens of *T. amazonica* that he recently collected. Dr. M. Graham Netting of the Carnegie Museum tried to locate the holotype of *T. quadrizonata.* Mr. Harvey R. Bullis and Richard B. Roe of the Bureau of Commercial Fisheries Exploratory Fishing Base, Pascagoula, Mississippi, expedited the sending of specimens and data for *Thalassophryne* collected by the R/V Oregon. The illustrations showing the patterns important in distinguishing the species of *Thalassophryne* were prepared by Mrs. Mildred H. Carrington. Radiographs were taken by Messrs. Gordon Brooks, Robert E. Jenkins, and Anthony H. Pierce, Jr. The manuscript was read by Drs. Daniel M. Cohen, Robert H. Gibbs, Jr., John E. Randall, and Victor G. Springer.

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Addendum: After submission of this paper, Sr. Francisco Mago Leccia informed me that fishermen in central Venezuela at times refer to *T. maculosa* as "mataperro" (dogkiller) because dogs sometimes die from wounds inflicted by *T. maculosa* while browsing among the fishermen's catch. Sr. Mago Leccia has a record of a man of 60 whose left thumb was punctured through a rubber glove while preserving a *T. maculosa*. Severe pain resulted within a few minutes. An hour later the man felt as if seasick and went to bed to relieve this sensation. The thumb became swollen and violet spots appeared on the palm and fingers of his left hand. A fever developed and sensation was lost in the thumb. During the first day, there was frequent urination. The next day the man cut the wound open relieving some of the pain. The following day the swelling began to abate but pain continued. It took 7 days for him to recover completely.

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Belonion, a New Genus of Fresh-water Needlefishes from South America

BY BRUCE B. COLLETTE[1]

INTRODUCTION

While preparing the sections on needlefishes and halfbeaks for "Fishes of the western North Atlantic," I examined two collections containing two new species that represent a new genus of needlefishes (Belonidae). One of these collections is from the Río Atabapo, a tributary of the Orinoco River on the Venezuela-Colombia border. The other is from the Rio Madeira, a tributary of the Amazon in Brazil. After completion of the first draft of this manuscript, an additional series of the second new species, recently collected in a tributary of the Rio Madeira in Bolivia near the Brazilian border, became available to me. Until the present time, only three fresh-water species of synentognaths have been known from South America east of the Andes: one halfbeak, *Hyporhamphus brederi* (Fernández-Yépez), and two needlefishes, *Potamorrhaphis guianensis* (Schomburgk) and *Pseudotylosurus angusticeps* (Günther).

Mme. M. L. Bauchot and the late Dr. Paulo de Miranda Ribeiro kindly lent me the original series of both new species. Recently, Dr. Reeve M. Bailey collected a fresh series of one of the new species, and he has graciously permitted me to report on these. This material was collected on the American Museum-Bolivian Expedition of 1964, sup-

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ported by Grant No. DA-MD-49-193-63-G82 of the United States Army Medical Research and Development Command, Office of the Surgeon General, and by the National Geographic Society and the American Museum of Natural History. Drs. E. H. Ahlstrom and Stanley H. Weitzman have assisted me with parts of the osteological work. Specimens were cleared and stained with the trypsin digestion method devised by Dr. W. Ralph Taylor. Messrs. Robert E. Jenkins, Harold Lazard, and Anthony H. Pierce, Jr., made the radiographs. Drs. Daniel M. Cohen, Robert H. Gibbs, Jr., William A. Gosline, John E. Randall, Donn E. Rosen, and Mr. Frederick H. Berry have commented on drafts of the manuscript. The figures of the new species were drawn by Mrs. Mildred H. Carrington. The figures of pharyngeal teeth, caudal skeletons, and interorbital canals were prepared by the author with the aid of a camera lucida and were inked and shaded by Mrs. Carrington. This paper is the fifth in a series on the systematics of synentognath (beloniform) fishes.

MATERIALS AND METHODS

Type materials of the new species are in the following collections:

A.M.N.H., the American Museum of Natural History
M.N.H.N., Museum National d'Histoire Naturelle, Paris
M.N.R.J., Museu Nacional, Rio de Janeiro, Brazil
U.S.N.M., United States National Museum, Smithsonian Institution

The specimens of *Belonion dibranchodon* are very soft; the specimens of *B. apodion* from both series are better preserved but are distorted. Therefore it was difficult to obtain accurate measurements. The body length from the posterior margin of the opercle to the base of the caudal fin is used as the indication of size rather than the standard length which includes the length of the frequently broken upper jaw. In order to emphasize the few morphometric differences, most of the measurements have been converted into per cent of head length for presentation. Head length was measured from the tip of the upper jaw to the posterior margin of the opercle.

In addition to examining the type material of the two new species, many preserved specimens, and radiographs of more than 1000 specimens representing 28 of the approximately 30 genera of synentognaths, I have partially dissected cleared and stained specimens of 24 genera which served as the primary basis for the comparative part of this paper. The number of cleared and stained specimens examined follows the name of the species.

Belonidae
  Belone belone (Linnaeus), two
  Tylosurus crocodilus (Peron and LeSueur), one
  Ablennes hians (Valenciennes), two
  Platybelone argalus (LeSueur), one
  Strongylura notata (Poey), two
  Strongylura marina (Walbaum), five
  Pseudotylosurus angusticeps (Günther), one
  Xenentodon cancila (Hamilton-Buchanan), one
  Potamorrhaphis guianensis (Schomburgk), four
  Belonion dibranchodon, new species, one
  Belonion apodion, new species, four
Scomberesocidae
  Scomberesox saurus (Walbaum), two
  Cololabis saira (Brevoort), four
  Cololabis adocoetus Böhlke, four
Hemiramphidae
  Hemiramphus brasiliensis (Linnaeus), two
  Hyporhamphus picarti (Valenciennes), 10
  Hyporhamphus species, 10
  Arrhamphus sclerolepis (Günther), one
  Chriodorus atherinoides Goode and Bean, four
  Euleptorhamphus velox Poey, two
  Zenarchopterus gilli Smith, three
  Zenarchopterus buffonis (Valenciennes), one
  Dermogenys species, one
  Hemirhamphodon pogonognathus (Bleeker), one
  Oxyporhamphus micropterus (Valenciennes), two
Exocoetidae
  Fodiator acutus (Valenciennes), one
  Parexocoetus brachypterus (Richardson), four
  Exocoetus obtusirostris Günther, five
  Exocoetus volitans Linnaeus, two
  Danichthys rondeletii (Valenciennes), five

This material is, or will be, deposited in the United States National Museum.

To facilitate comparison of *Belonion* with the other synentognath genera, the genera are listed in tables 1–3 in order of what I consider to be increasing specialization, insofar as this can be expressed in a linear sequence. The first two families (Belonidae and Scomberesocidae) form the suborder Scomberesocoidei (superfamily Scomberesocoidea of Rosen, 1964) which differs from the Exocoetoidei (superfamily Exocoetoidea of Rosen), composed of the Hemiramphidae and Exocoetidae, primarily by having the third pair of upper pharyngeal bones completely separate, not fused or closely joined. My ideas for the arrangement of the genera are based partly on my unpublished studies on the Belonidae and Hemiramphidae and partly on the literature (Regan, 1911;

TABLE 1

Total Number of Vertebrae in Genera of Synentognathi

	35	37	39	41	43	45	47	49	51	53	55	57	59	61	63	65	67	69	71	73	75	77	79	81	83	85	87	89	91	93	95	97
Belonidae																																
Belone	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	x	x	x	x	—	—	—	—	—	—	—	—
Petalichthys	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	x	—	—	—	—	—	—	—	—	—	—	—	—	—
Tylosurus	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	x	x	x	x	x	x	x	x	x	x	x	x	x	x	—	—
Ablennes	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	x	x	x	x	x	x	x	x	x
Platybelone	—	—	—	—	—	—	—	—	—	—	—	—	—	x	x	x	x	x	x	x	x	—	—	—	—	—	—	—	—	—	—	—
Strongylura	—	—	—	—	—	—	—	—	—	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	—	—	—	—	—
Xenentodon	—	—	—	—	—	—	—	—	—	—	—	x	x	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Pseudotylosurus	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	x	x	x	—	—	—	—	—	—	—	—	—	—	—	—
Potamorrhaphis	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	x	x	x	x	x	x	—	—	—	—	—	—	—	—	—	—	—
Belonion dibranchodon	—	—	—	—	—	—	—	—	—	—	—	x	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Belonion apodion	—	—	—	—	—	—	—	—	x	x	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Scomberesocidae																																
Scomberesox	—	—	—	—	—	—	—	—	—	—	—	—	—	—	x	x	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
New genus Hubbs and Wisner	—	—	—	—	—	—	—	—	—	—	—	x	x	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Cololabis	—	—	—	—	—	—	—	—	—	—	—	—	—	—	x	x	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
New genus Hubbs and Wisner	—	—	—	—	—	—	—	—	—	x	x	x	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—

TABLE 1—(*Continued*)

	35	37	39	41	43	45	47	49	51	53	55	57	59	61	63	65	67	69	71	73	75	77	79	81	83	85	87	89	91	93	95	97
HEMIRAMPHIDAE																																
Hemiramphus	—	—	—	—	—	—	—	—	x	x	x	x	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Hyporhamphus	—	—	—	—	—	x	x	x	x	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Odontorhamphus	—	—	—	—	—	—	—	—	—	x	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Arrhamphus	—	—	—	—	—	—	—	—	x	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Chriodorus	—	—	—	—	—	—	—	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Euleptorhamphus	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	x	x	x	—	—	—	—	—	—	—	—	—	—	—	—
Zenarchopterus	—	x	x	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Dermogenys	—	x	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Hemirhamphodon	—	—	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Oxyporhamphus	—	—	—	—	—	—	—	x	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
EXOCOETIDAE																																
Fodiator	—	x	x	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Parexocoetus	x	x	x	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Exocoetus	—	—	—	x	x	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Cypselurus	—	—	x	x	x	x	x	x	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Prognichthys	—	—	—	x	x	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Hirundichthys	—	—	—	—	x	x	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Danichthys	—	—	—	—	x	x	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—

TABLE 2
Number of Pectoral Rays in Genera of Synentognathi

	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
BELONIDAE																
Belone	—	—	—	—	—	—	—	x	x	x	—	—	—	—	—	—
Petalichthys	—	—	—	—	—	—	x	x	—	—	—	—	—	—	—	—
Tylosurus	—	—	—	—	—	—	—	—	x	x	x	—	—	—	—	—
Ablennes	—	—	—	—	—	—	—	x	x	x	x	—	—	—	—	—
Platybelone	—	—	—	—	—	x	x	x	x	—	—	—	—	—	—	—
Strongylura	—	—	—	—	x	x	x	x	x	—	—	—	—	—	—	—
Xenentodon	—	—	—	—	—	x	x	x	—	—	—	—	—	—	—	—
Pseudotylosurus	—	—	—	x	x	x	—	—	—	—	—	—	—	—	—	—
Potamorrhaphis	—	—	x	x	—	—	—	—	—	—	—	—	—	—	—	—
Belonion dibranchodon	x	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Belonion apodion	x	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—
SCOMBERESOCIDAE																
Scomberesox	—	—	—	—	—	—	—	—	x	x	—	—	—	—	—	—
New genus Hubbs and Wisner	—	—	—	—	—	x	x	—	—	—	—	—	—	—	—	—
Cololabis	—	—	—	—	—	—	—	—	x	x	—	—	—	—	—	—
New genus Hubbs and Wisner	—	—	—	x	x	x	x	—	—	—	—	—	—	—	—	—
HEMIRAMPHIDAE																
Hemiramphus	—	—	—	—	—	x	x	x	—	—	—	—	—	—	—	—
Hyporhamphus	—	—	—	x	x	x	x	x	—	—	—	—	—	—	—	—
Odontorhamphus	—	—	—	—	—	—	x	x	—	—	—	—	—	—	—	—
Arrhamphus	—	—	—	—	—	—	—	x	x	—	—	—	—	—	—	—
Chriodorus	—	—	—	—	—	—	—	x	x	x	—	—	—	—	—	—
Euleptorhamphus	—	—	x	x	x	—	—	—	—	—	—	—	—	—	—	—
Zenarchopterus	—	—	—	x	x	x	x	—	—	—	—	—	—	—	—	—
Nomorhamphus	—	—	—	—	—	—	—	x	—	—	—	—	—	—	—	—
Dermogenys	—	—	—	—	x	x	x	x	—	—	—	—	—	—	—	—
Hemirhamphodon	—	—	—	x	x	—	—	—	—	—	—	—	—	—	—	—
Oxyporhamphus	—	—	—	—	—	—	x	x	x	—	—	—	—	—	—	—
EXOCOETIDAE																
Fodiator	—	—	—	—	—	—	—	—	x	x	x	x	—	—	—	—
Parexocoetus	—	—	—	—	—	—	—	x	x	x	—	—	—	—	—	—
Exocoetus	—	—	—	—	—	—	—	—	—	x	x	x	x	—	—	—
Cypselurus	—	—	—	—	—	—	—	x	x	x	x	x	x	—	—	—
Prognichthys	—	—	—	—	—	—	—	—	—	—	—	—	x	x	x	—
Hirundichthys	—	—	—	—	—	—	—	—	—	—	x	x	x	x	x	x
Danichthys	—	—	—	—	—	—	—	—	—	—	—	x	x	x	x	x

Nichols and Breder, 1928; Breder, 1932, 1938; Böhlke, 1951; and Parin, 1961). The names used for the Belonidae follow Collette and Berry (1965) rather than Mees (1962, 1964). Only the range of variation is given in tables 1–3 because the tables are intended to show only broad

TABLE 3

Number of Branchiostegal Rays in Genera of Synentognathi

	6	7	8	9	10	11	12	13	14	15
BELONIDAE										
Belone	—	—	—	—	—	—	x	x	—	—
Petalichthys	—	—	—	—	—	—	x	—	—	—
Tylosurus	—	—	—	—	—	—	—	—	x	x
Ablennes	—	—	—	—	—	—	x	x	—	—
Platybelone	—	—	—	—	x	x	—	—	—	—
Strongylura	—	—	—	—	—	—	x	x	x	x
Xenentodon	—	—	—	—	—	x	—	—	—	—
Pseudotylosurus	—	—	x	—	—	—	—	—	—	—
Potamorrhaphis	—	—	—	—	x	x	—	—	—	—
Belonion dibranchodon	x	x	—	—	—	—	—	—	—	—
Belonion apodion	x	x	—	—	—	—	—	—	—	—
SCOMBERESOCIDAE										
Scomberesox	—	—	—	—	—	—	—	x	x	x
New genus Hubbs and Wisner	—	—	—	—	x	x	x	—	—	—
Cololabis	—	—	—	—	—	—	x	x	x	x
New genus Hubbs and Wisner	—	—	—	x	x	x	—	—	—	—
HEMIRAMPHIDAE										
Hemiramphus	—	—	—	—	—	—	x	x	—	—
Hyporhamphus	—	—	—	—	x	x	x	x	—	—
Odontorhamphus	—	—	—	—	—	x	x	x	—	—
Arrhamphus	—	—	—	—	—	—	x	x	x	—
Chriodorus	—	—	—	—	—	—	x	x	—	—
Euleptorhamphus	—	—	—	—	—	—	—	x	x	—
Zenarchopterus	—	—	x	x	x	x	—	—	—	—
Dermogenys	—	—	—	—	x	—	—	—	—	—
Hemirhamphodon	—	—	x	x	—	—	—	—	—	—
Oxyporhamphus	—	—	—	—	x	x	x	x	—	—
EXOCOETIDAE										
Fodiator	—	—	—	x	x	x	—	—	—	—
Parexocoetus	—	—	—	x	x	x	x	x	—	—
Exocoetus	—	—	—	x	x	x	x	—	—	—
Cypselurus	—	—	—	x	x	x	x	x	—	—
Prognichthys	—	—	x	x	x	x	x	—	—	—
Hirundichthys	—	—	—	x	x	x	x	—	—	—
Danichthys	—	—	—	—	x	x	x	—	—	—

evolutionary trends. The data for these tables are partly original and partly from the literature (Breder, 1938; Bruun, 1935; Parin, 1961).

BELONION, NEW GENUS

Type Species: *Belonion apodion*, new species.

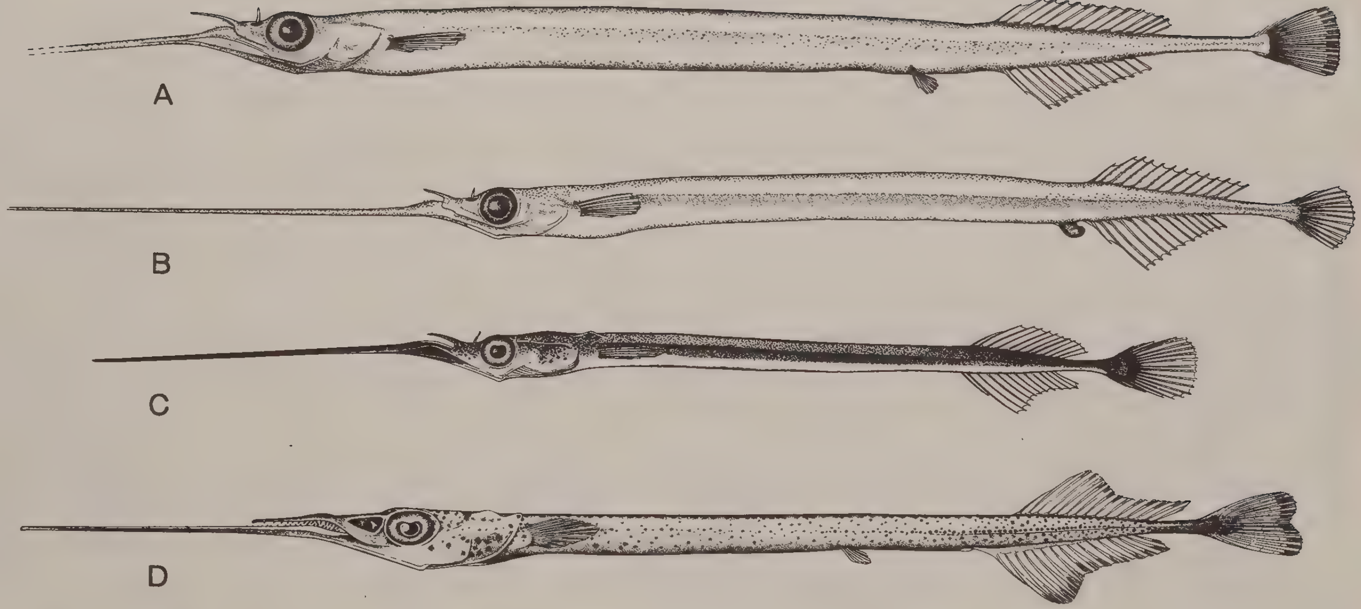

Fig. 1. A. Lateral view of paratype of *Belonion dibranchodon,* new species, U.S.N.M. No. 199463, Venezuela, Río Atabapo, 38.2 mm. in body length. B. Lateral view of paratype of *Belonion apodion,* new species, U.S.N.M. No. 199540, Brazil, Borba, 29.4 mm. in body length. C. Lateral view of holotype of *B. apodion,* new species, A.M.N.H. No. 20805, Bolivia, 3 kilometers southwest of Costa Margues, Brazil, female, 40.1 mm. in body length. D. Lateral view of juvenile of *Strongylura marina,* U.S.N.M. No. 189006, Nicaragua, 23.5 mm. in body length.

Diagnosis: Epipleurals absent (present in all other genera of Synentognathi). Fourth pair of upper pharyngeal bones absent (present in other genera of Scomberesocoidei except *Xenentodon,* absent from all genera of Exocoetoidei). Branchiostegal rays 6 or 7 (as low as 8 only in *Pseudotylosurus, Zenarchopterus, Hemirhamphodon,* and *Prognichthys,* 9–15 in other genera; table 3). Pectoral rays 5 or 6 (7–8 in *Potamorrhaphis,* 8–10 in *Pseudotylosurus,* 7–9 in *Euleptorhamphus,* 8–19 in other genera; table 2). Pleural ribs attached to second vertebra (on third in all other synentognaths except on second in *Hemirhamphodon,* and on fourth or fifth in *Pseudotylosurus.* Precaudal vertebrae 32–37, caudal vertebrae 19–23, total 52–59 (table 1). An elongate nasal barbel present. Preorbital canal a simple tube with three pores and no branches. Lower jaw very long (50% to 60% of body length) and upper jaw short. Second pair of upper pharyngeal bones present or absent. Principal caudal rays 7+8 or 6+7. Reproductive maturity attained at a small size (about 25 mm. body length).

Description: Head length 18 per cent to 23 per cent of body length. Snout length 29 per cent to 38 per cent of head length; postorbital distance 35 per cent to 45 per cent of head length; length of preopercle 11 per cent to 18 per cent of head length; length of orbit 23 per cent to 29 per cent of head length; interorbital width 17 per cent to 25 per cent of head length; head depth just posterior to orbit 23 per cent to 28 per cent of head length; head width just posterior to orbit 26 per cent to 31 per cent of head length; pectoral fin length 41 per cent to 51 per cent of head length.

Etymology: The neuter diminutive is from the Greek *belone,* needle, in reference to the small size of both species in the genus.

Belonion dibranchodon, new species

Figure 1A

Holotype: M.N.H.N. No. 87–836, 34.0 mm. in body length, 36.9 mm. in standard length; Venezuela, Río Atabapo, a tributary of the Orinoco River on the border between the state of Amazonas, Venezuela, and Vaupes, Colombia; M. Chaffanjon; 1887.

Paratypes: M.N.H.N. No. B.2529 (seven, 30.4–33.1 mm. in body length), U.S.N.M. No. 199463 (seven, 27.1–38.2 mm. in body length), and A.M.N.H. No. 20808 (one, 32.1 mm. in body length); all from the type locality.

Diagnosis: A species of *Belonion* with pelvic fins and pelvic girdle present; 7+8 principal caudal rays; 34–37 precaudal, 22–23 caudal, and 57–59 total, vertebrae; first pair of upper pharyngeal bones absent, second and third toothed; 12–14 dorsal rays, usually 14; 12–15 anal rays, usually 14 or 15. The interorbital canals are joined together (fig. 7D).

Description: Meristic data for *Belonion dibranchodon* are compared with those for *B. apodion* in tables 4 and 5; morphometric data are given in table 6. *Belonion dibranchodon* has a narrower interorbital width (17% to 22% of head length, $\bar{x}$ 18.3, versus 20% to 25%, $\bar{x}$ 21.6); a shorter post-orbital distance (35% to 40% of head length, $\bar{x}$ 37.4, versus 38% to 45%, $\bar{x}$ 40.8), and a slightly longer snout (30% to 38% of head length, $\bar{x}$ 33.8, versus 30% to 34%, $\bar{x}$ 31.4).

TABLE 4

Number of Fin Rays in *Belonion dibranchodon* and *B. apodion*

	B. dibranchodon	*B. apodion*	
		Brazil	Bolivia
Dorsal fin rays			
11	—	5	—
12	1	24	2[a]
13	3	13	5
14	12[a]	1	—
Anal fin rays			
12	1	10	—
13	2	25	5[a]
14	8[a]	8	2
15	5	—	—

[a] Holotypes.

There are three longitudinal bands of pigment on the dorsum, sides, and venter. The band on the dorsum extends from the head to the base of the caudal fin along the middorsal line. It appears as two lines, because the smallest melanophores on the middorsal line have mostly faded. This pigment band is darker around the dorsal fin base. The lateral band is faint (fig. 1A) and composed of very small melanophores as in the Brazilian series of *Belonion apodion.* The ventral band is moderately wide and is composed of medium-sized melanophores. The band is wider than that of either of the two series of *B. apodion,* and the melanophores are somewhat smaller. The band becomes darker just anterior to the urogenital area, where it divides into two bands that continue on each side of the anal fin base and become lighter.

The pectoral, pelvic, and anal fins lack pigment, but there are a few melanophores on the pectoral fin base. The dorsal fin is mostly immaculate, but there are scattered melanophores on a few of the rays. There is a faint subterminal band on the caudal fin.

LOCALITY: These specimens are part of a collection made by Chaffanjon in the Orinoco and sent to the Paris museum in June, 1887. The exact locality of this collection is not known, but it was in the Río Atabapo which extends only about 70 miles along the Venezuela-Colombia border from the point where smaller streams come together on the south to its junction with the Orinoco proper on the north.

TABLE 5

NUMBER OF VERTEBRAE IN *Belonion dibranchodon* AND *B. apodion*

	B. dibranchodon	*B. apodion*	
		Brazil	Bolivia
Precaudal vertebrae			
32	—	1	—
33	—	10	1
34	1	17	3[a]
35	8[a]	2	3
36	5	—	—
37	2	—	—
Caudal vertebrae			
19	—	10	1
20	—	14	2[a]
21	—	5	4
22	9[a]	1	—
23	7	—	—
Total vertebrae			
52	—	2	1
53	—	15	—
54	—	9	3[a]
55	—	4	2
56	—	—	—
57	4[a]	—	—
58	9	—	—
59	3	—	—

[a] Holotypes.

Pellegrin (1903a, 1908, 1909, 1912) described a number of new species from Chaffanjon's Orinoco collections: a cichlid, *Pterophyllum altum;* three characins, *Hemiodus argenteus, Anastomoides atrianalis,* and *Brycon bicolor;* and a catfish, *Xenocara macrophthalma.* Pellegrin (1903b), in his revision of the Cichlidae, utilized material of five more species from Chaffanjon's collections: *Acaropsis nassa* (Heckel), *Cichla ocellaris* Bloch and Schneider, *Cichla temensis* Humboldt, *Cichlasoma insigne* (Heckel), and *Crenicichla brasiliensis* (Bloch) (three of Heckel's "varieties," *lenticula, lugubris,* and *johanna*).

TABLE 6

Comparison of Morphometric Characters of *Belonion dibranchodon* and two Populations of *Belonion apodion*

(Head length in per cent of body length; other measurements in per cent of head length.)

	B. dibranchodon (*N*=9)		*B. apodion,* Brazil (*N*=8)		*B. apodion,* Bolivia (*N*=7)	
	x̄	Range	x̄	Range	x̄	Range
Body length (mm.)	32.8	28.5–38.2	30.2	26.4–35.3	37.2	33.5–41.8
Standard length (mm.)	39.6	34.0–47.5	36.3	31.5–42.4	45.1	38.2–50.0
Head length	20.5	18.7–22.8	21.4	19.7–22.8	20.6	18.2–22.3
Snout length	33.8	30.5–37.9	31.6	29.8–33.8	31.2	29.2–33.8
Postorbital distance	37.4	35.2–40.0	41.1	37.5–43.7	40.5	39.2–45.0
Preopercle length	14.8	13.8–16.7	14.1	12.3–18.3	12.5	11.2–14.8
Orbital length	26.4	23.9–27.7	26.8	24.7–28.1	25.7	22.8–28.8
Interorbital width	18.3	16.9–21.8	21.3	19.7–23.4	22.0	19.7–25.0
Head depth	25.7	23.3–27.7	26.3	24.7–28.1	25.6	23.6–27.9
Head width	28.6	26.0–30.0	27.9	26.0–29.8	28.1	25.8–30.6
Pectoral length	45.4	41.1–50.9	45.0	43.1–47.4	44.9	41.8–47.5
Pelvic length	12.3	10.5–14.1	No pelvic fins		No pelvic fins	

Etymology: From the Greek *di-*, two, *branchos,* gill, and *odontos,* tooth, in reference to the two pairs of toothed upper pharyngeal bones.

Belonion apodion, new species

Figure 1B, C

Holotype: A.M.N.H. No. 20805, female, 40.1 mm. in body length, 48.2 mm. in standard length; Bolivia, laguna 3 kilometers southwest of Costa Margues, Brazil, Río Guaporé; October 1, 1964; R. M. Bailey field number 64–48.

Paratypes: A.M.N.H. No. 20806 (three, 34.1–37.1 mm. in body length) and U.S.N.M. No. 199539 (three, 33.5–41.8 mm. in body length), collected with the holotype. M.N.R.J. No. 4490 (82, 22.3–29.7 mm. in body length), U.S.N.M. No. 199540 (28, 21.0–37.9 mm. in body length), M.N.H.N. No. 66–725 (two, 25.3–27.1 mm. in body length), and A.M.N.H. No. 20807 (two, 25.5–30.4 mm. in body length), Brazil, Estado Amazonas, Lago Acara, Borba, Madeira River drainage, a tributary of the Amazon; A. Parko; September, 1943.

Diagnosis: A species of *Belonion* without pelvic fins and pelvic girdle; 6+7 principal caudal rays; 32–35 precaudal, 19–22 caudal, and 52–56 total, vertebrae; first and second pair of upper pharyngeal bones absent, third pair toothed; 11–14 dorsal rays, usually 12; 12–14 anal rays; interorbital canals separate from each other (fig. 7C).

Description: Meristic and morphometric data for *Belonion apodion* and *B. dibranchodon* are compared in tables 4–6. *Belonion apodion* has a wider interorbital distance, a longer postorbital distance, and a slightly shorter snout.

There are three lateral pigment bands on the body of *Belonion apodion* as in *B. dibranchodon.* The Bolivian series is fresher and better preserved than the Brazilian series and differs in pigmentation mainly in having the melanophores more expanded. The Brazilian series has an even band of medium-sized melanophores on the dorsum, about 10 melanophores wide. The melanophores in the dorsal band of the Bolivian series are so expanded that they nearly fuse together to form a black stripe. The lateral band is even on its dorsal edge in the Brazilian series and irregular ventrally. The melanophores are much smaller than in the dorsal band. The lateral band in the Bolivian series is even and well defined ventrally, but the band gradually grades into the dorsal band above. The melanophores are much smaller, and there is more space between individual melanophores than in the dorsal band. The ventral band in both series is quite narrow and consists of medium-sized melanophores. The ventral band passes laterally to the immaculate urogenital region. The band is variable in intensity along the anal base and may become a solid black stripe in some specimens in the Bolivian series.

In the Brazilian series, the pectoral and anal fins lack pigment, but there is a concentration of melanophores surrounding the dorsal half of the pectoral fin base. A few scattered melanophores are present in some specimens on the anterior and posterior surfaces of the dorsal fin rays. In the Bolivian series, pigment around the base of the pectoral fin forms a crescent dorsoposteriorly. Small melanophores outline the pectoral rays. Most of the first three anal rays and the distal two-thirds of the other anal rays have melanophores. Melanophores are present all over the dorsal fin rays, and a few are present on the basal part of the dorsal fin membranes. The rays of the caudal fin are outlined by melanophores.

Maturity: The Brazilian specimens more than 24.5 in body length are apparently mature. Most are females with small eggs. The smaller Brazilian specimens (22.8–24.5 mm. in body length) are immature. All the Bolivian specimens examined are mature, and the largest two (40.1–41.8 mm. in body length) have much larger (0.3 mm. in diameter) eggs than any of the Brazilian specimens, so may be nearly ripe.

Etymology: From the Greek *a,* without, and *podos,* foot, in reference to the absence of pelvic fins and girdle.

DISCUSSION

By definition, *Belonion* belongs to the suborder Scomberesocoidei (superfamily Scomberesocoidea of Rosen, 1964) because it has the third pair of upper pharyngeal bones separate (fig. 2); in the Exocoetoidei (superfamily Exocoetoidea of Rosen), these bones are joined together in a manner analogous to the fusion of the lower pharyngeal bones throughout the Synentognathi. *Belonion* lacks the dorsal and anal finlets diagnostic of the Scomberesocidae.

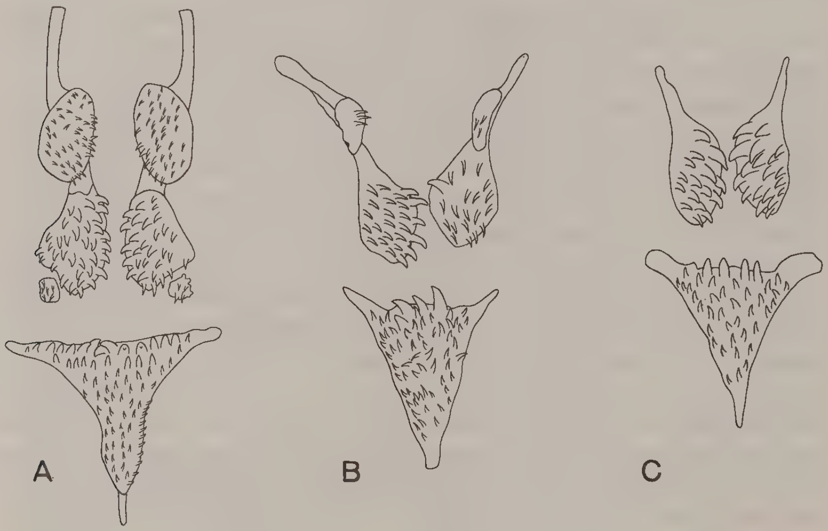

Fig. 2 Pharyngeal teeth. A. *Potamorrhaphis guianensis.* B. *Belonion dibranchodon.* C. *Belonion apodion. Potamorrhaphis* has all three pairs of upper pharyngeal bones; *B. dibranchodon* has the second and third pairs; and *B. apodion* has only the third pair.

Superficially, *Belonion* resembles a hemiramphid because of its short upper jaw and elongate lower jaw. All Belonidae go through a "halfbeak" stage during ontogeny (fig. 1D), and some, such as *Platybelone argalus,* have a relatively short upper jaw even as adults (Berry and Rivas, 1962, fig. 1a). All known specimens of *Belonion* are small (largest 41.8 mm. in body length, 50.0 mm. in standard length), and they retain the short upper jaw, characteristic of juveniles of other needlefishes, into maturity. Thus, *Belonion* may be considered a paedomorphic or neotenic species with regard to size and retention of a short upper jaw. This is the third case of paedomorphism in the order. Nichols and Breder (1928) suggested that the scomberesocid genus *Cololabis* is a permanently arrested stage in the ontogenetic development of *Scomberesox.* Böhlke (1951) described *Cololabis adocoetus* as having evolved from *C. saira* by the loss of pectoral rays and gill rakers. Hubbs and Wisner (MS) consider *C. adocoetus* to be generically distinct from *C. saira* because of its small size and reduced numbers of vertebrae, pectoral fin rays, and branchiostegal rays. They also will describe a new genus and species that has similarly evolved through arrested development from *Scomberesox.*

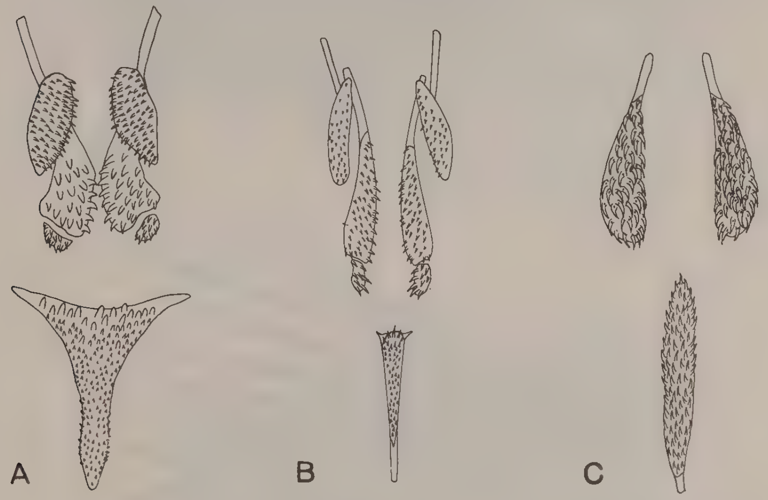

Fig. 3. Pharyngeal teeth. A. *Strongylura notata.* B. *Pseudotylosurus angusticeps.* C. *Xenentodon cancila. Xenentodon* has only the third upper pair of pharyngeal bones.

In its reduced pharyngeal dentition (fig. 2) and in the number of vertebrae (table 1), pectoral rays (table 2), and branchiostegal rays (table 3), *Belonion* shows tendencies similar to those apparent in the three other fresh-water genera of needlefishes (*Potamorrhaphis* and *Pseudotylosurus* from South America, and *Xenentodon* from Asia) and in the specialized, viviparous, brackish and fresh-water Indo-Australian genera of the Hemiramphidae (*Zenarchopterus, Dermogenys,* and *Hemirhamphodon*).

Xenentodon and *Belonion apodion* have the most reduced pharyngeal

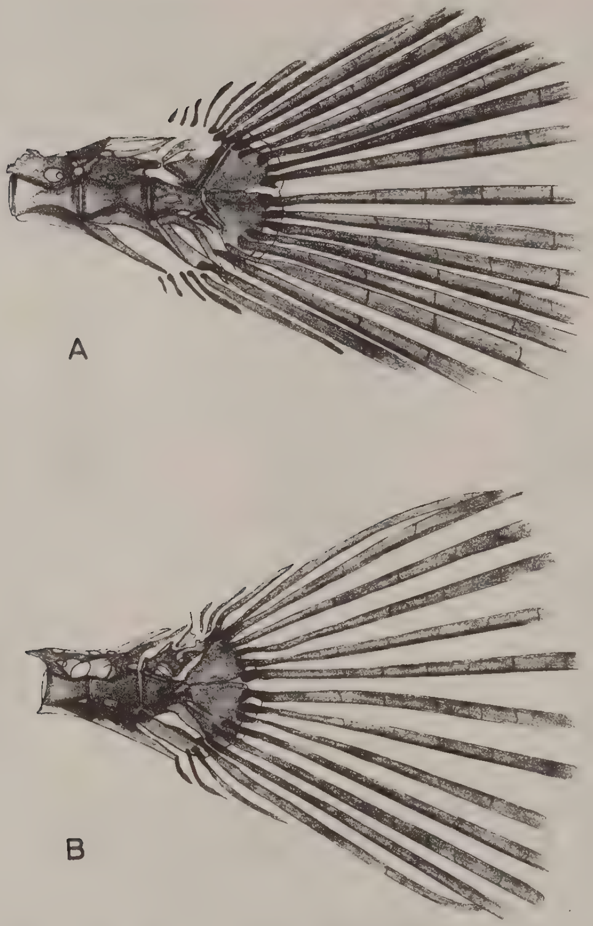

Fig. 4. Caudal skeletons. A. *Belonion dibranchodon* with 7+8 principal caudal rays. B. *Belonion apodion* with 6+7 principal caudal rays. The penultimate centrum of *B. apodion* is abnormal.

dentition in the order. Both lack all but the third pair of upper pharyngeal bones. The shapes of the tooth patches on these bones in *Xenentodon* (fig. 3C), however, are different from those of all other species of the Belonidae, including *Belonion apodion.* Therefore, it is clear that the loss of teeth was independent in the two genera. The lower pharyngeal plate of *Xenentodon* is also strikingly different from that of any other synentognaths in lacking any trace of the triangular expansion at the posterior

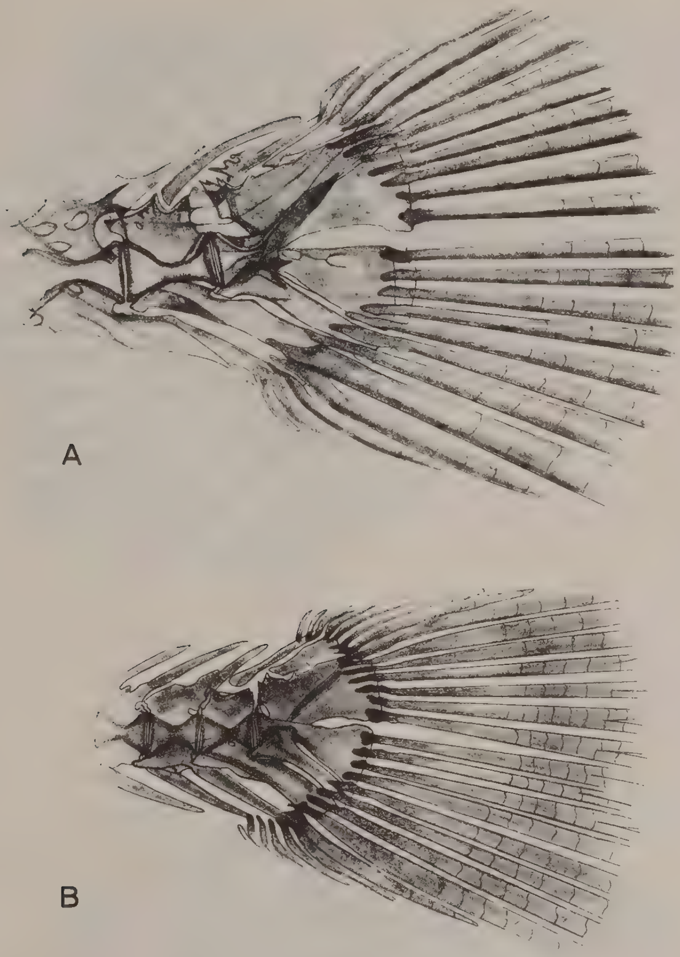

Fig. 5. Caudal skeletons. A. *Strongylura notata.* B. *Xenentodon cancila.*

end of the bone. *Xenentodon* does not show a reduction in number of pectoral or branchiostegal rays (tables 1, 2), and its caudal structure (fig. 5) is typical of most other genera of the Belonidae.

A number of characters show a close relationship between *Belonion* and *Potamorrhaphis.* In pharyngeal dentition, there seems to be a progressive reduction from *Potamorrhaphis* to *Belonion dibranchodon* to *B. apodion.* The shapes of the third upper pharyngeal bones and the lower pharyngeal plate and the teeth on them are very similar in both genera (fig. 2).

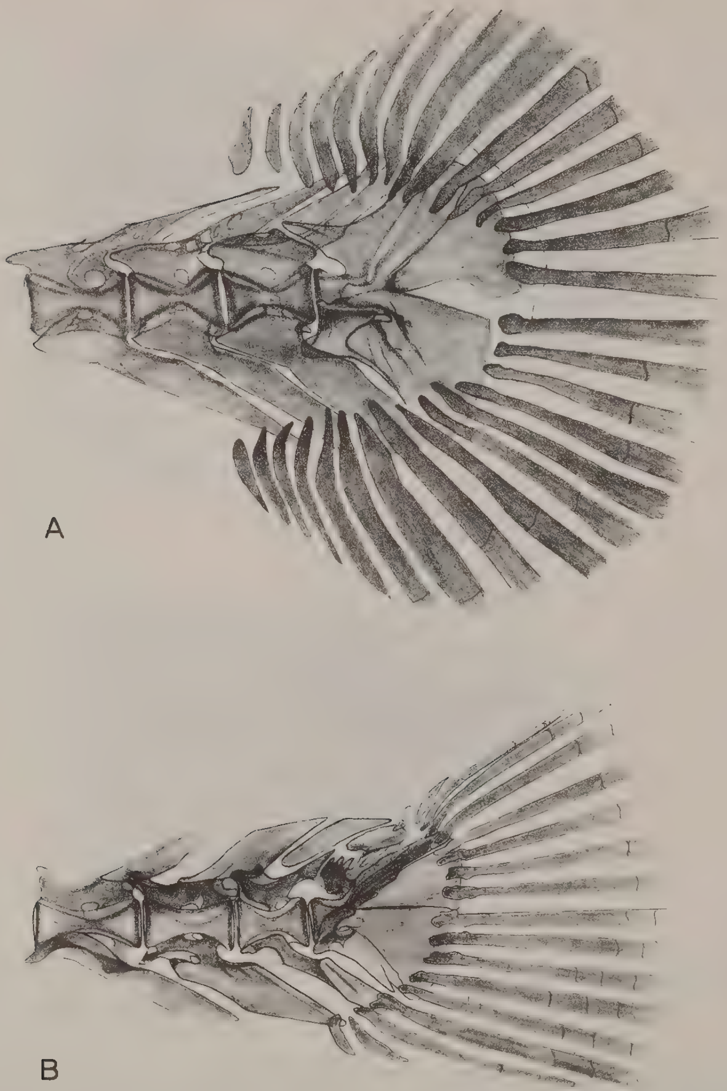

Fig. 6. Caudal skeletons. A. *Pseudotylosurus angusticeps.* B. *Potamorrhaphis guianensis.*

Belonion dibranchodon has lost the small fourth upper pharyngeals present in *Potamorrhaphis* and other needlefishes and has the dentition and size of the second upper pharyngeals reduced. The second pharyngeals have disappeared in *Belonion apodion.*

In both *Belonion* and *Potamorrhaphis* the anterior projection of the flattened first neural spine fits between the prominent flanges of the exoccipital and the paired supraoccipital crests. The position of the first neural spine relative to the supraoccipital crests varies widely in the other genera of synentognaths but none of these variations resemble the condition in *Belonion* and *Potamorrhaphis.* The degree of expansion of the first neural spine varies among the genera. Most synentognaths have two supraoccipital crests, as Rosen (1964, p. 231) noted, but there are a few exceptions. According to Parin (1961, p. 123), *Exocoetus monocirrhus* has only one crest, although *E. volitans* and *E. obtusirostris* have the usual two crests. At least one species of *Hemiramphus* (*H. brasiliensis*) and one species of *Hyporhamphus* (*H. picarti*) have three crests. *Oxyporhamphus* also has three crests, as Parin noted (1961, p. 123).

Potamorrhaphis further resembles *Belonion* in its reduced number of pectoral rays (seven to eight versus five to six) but differs in having more branchiostegal rays (10–11). The most obvious meristic differences between the two genera are the large number of dorsal (29–34) and anal (26–30) rays in *Potamorrhaphis. Belonion* has a more usual count for needlefishes (dorsal 11–14, anal 12–15).

The majority of synentognaths have 7 + 8 principal and 6 + 7 branched caudal rays. The eighth principal ventralmost caudal ray frequently inserts over the expanded last haemal spine, and the seventh principal ventral ray does so, at least partially, in some species (figs. 5–6). The fresh-water genera of needlefishes and the brackish-water and fresh-water genera of halfbeaks tend to have rounded tails in contrast to the lobed or forked tails of marine genera. This tendency is correlated with a reduction in the number of principal caudal rays in *Potamorrhaphis* (fig. 6B) and in *Belonion apodion* (fig. 4B).

Within the Belonidae, there is relatively little variation in the pattern of the interorbital canals. *Strongylura notata* (fig. 7A) and *Potamorrhaphis* (fig. 7B) are representative of the family. Not unexpectedly, *Belonion apodion* has the anterior portion of the canal reduced (fig. 7C). However, the canal in *B. dibranchodon* (fig. 7D) is unlike that of any other synentognath. The left and right canals are joined together so that median pores are present as well as the usual lateral pores. Superficially, the canal is similar to that of preserved specimens of *Hemirhamphodon,* but in *Hemiramphodon* this is due to the great reduction of bone in the cranial elements of the anterior portion of the canal, and not to fusion of the left and right canals, as is the case in *B. dibranchodon.*

Within the Synentognathi, two trends in vertebral number are apparent (table 1). The number increases with increasing specialization in the

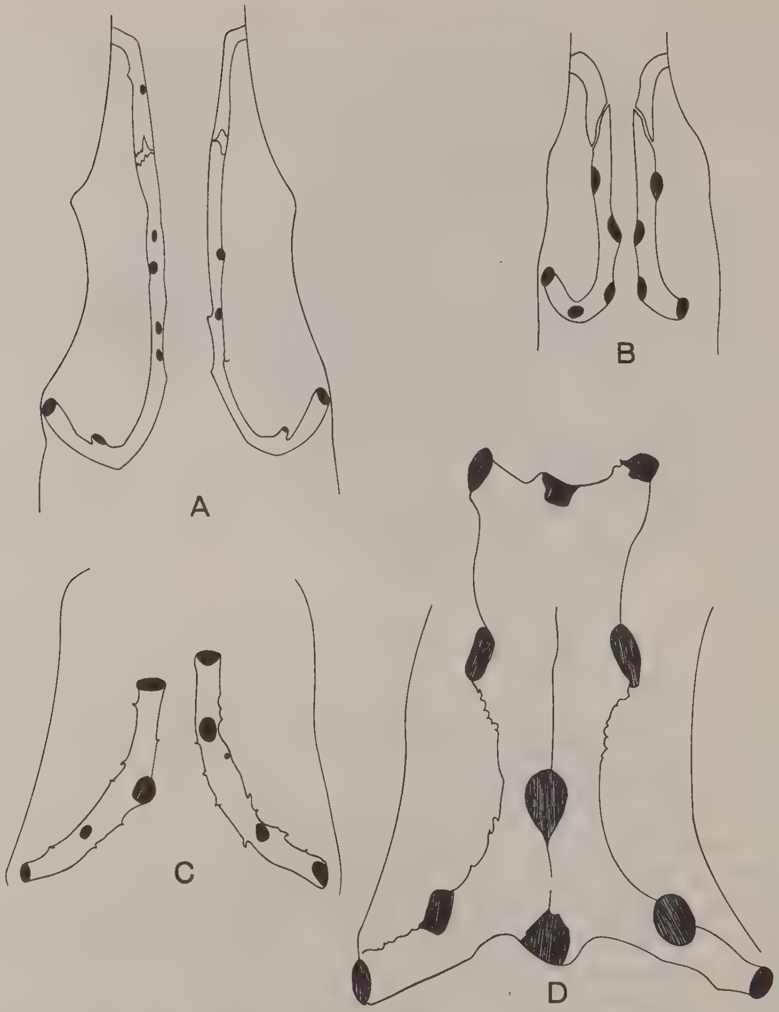

FIG. 7. Interorbital canals. A. *Strongylura notata.* B. *Potamorrhaphis guianensis.* C. *Belonion apodion.* D. *Belonion dibranchodon.*

Exocoetidae. The number is reduced in the two neotenic genera of Scomberesocidae (Hubbs and Wisner, MS). In the Hemiramphidae, both increase and decrease are associated with specialization. The pelagic genus *Euleptorhamphus* has 10–14 more vertebrae than any other genus, whereas *Zenarchopterus, Dermogenys,* and *Hemirhamphodon* have four to eight fewer. The Belonidae also show both trends. *Ablennes* has an increased number and is an ecological parallel of *Euleptorhamphus*. The trend toward reduction is shown in two species of *Strongylura* (*notata* and *urvillii*), *Xenentodon*, and *Belonion*. *Belonion dibranchodon* has about the same number of vertebrae as *Xenentodon*, *S. notata*, and *S. urvillii*. *Belonion apodion* has fewer vertebrae than any other species in the family.

The absence of epipleurals from both species of *Belonion* is a unique character in the Synentognathi. As Rosen (1964, p. 242) noted, most synentognaths have the first pleural rib articulating with the third vertebra. *Belonion* is an exception in having the first pleural rib on the second vertebra. The one cleared and stained specimen of *Pseudotylosurus* has the first pleural rib on the fourth vertebra on one side and on the fifth on the other side. The halfbeak *Hemirhamphodon* is the only other synentognath that has the first pleural rib on the second vertebra.

On the basis of the evidence presently available, I interpret the evolution of *Belonion* as follows: Inshore or neritic marine needlefishes similar to *Strongylura*, with three pairs of toothed upper pharyngeal bones, a moderate number of pectoral rays and vertebrae, a truncate caudal fin, and unforked pelvic fins smaller than the pectoral fins, moved into the fresh waters of South America. There *Pseudotylosurus* evolved, with its peculiar spine-bearing scales, elongate pharyngeal plate, and reduced number of branchiostegal rays. Another line of development from the same stock led to the ancestors of *Potamorrhaphis* and *Belonion*, needlefishes having an association of the expanded first neural spine with the supraoccipital crests and exoccipital flange. The teeth on the pharyngeal bones became larger and fewer, the number of pectoral rays was reduced to seven or eight, and the caudal fin became distinctly rounded. From such a form the ancestors of *Potamorrhaphis* secondarily developed a larger number of caudal vertebrae and dorsal and anal rays, whereas the ancestors of *Belonion* continued to specialize by reduction—in number of vertebrae, branchiostegal rays, and pectoral rays. The small fourth pharyngeal bone disappeared, and the size of the second became greatly reduced. This is the stage reached by *Belonion dibranchodon*. *Belonion apodion* became still more specialized along the same evolutionary line. The number of vertebrae became further reduced, the pelvic fins and pelvic girdle were lost, the caudal fin lost two principal rays, and the small second pharyngeal bone disappeared. These changes resulted in the most specialized of all needlefishes—*B. apodion*.

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REVUE CRITIQUE DES TYPES DE SCOMBRIDAE DES COLLECTIONS DU MUSÉUM NATIONAL D'HISTOIRE NATURELLE DE PARIS

Par Bruce B. COLLETTE

Un nouvel examen des types de Scombridae des collections du Muséum de Paris a montré qu'il était nécessaire d'apporter un certain nombre de modifications au *Catalogue des types de Scombroidei* de Bauchot et Blanc (1961) et Blanc et Bauchot (1962). L'objet de ce travail est de préciser le statut et l'identité de ces types.

La dernière publication du *Code International de Nomenclature zoologique* (1964) nécessite une nouvelle interprétation des concepts utilisés par Bertin dans le premier de la série des Catalogues de types du Muséum de Paris. Le présent travail adopte les définitions suivantes du Code International.

Série-type : « La série-type d'une espèce se compose de tous les spécimens sur lesquels l'auteur fonde son espèce... » (Article 72 b).

Holotype ; « Si une espèce nominale est fondée sur un spécimen unique » ou « si un auteur mentionne dans la description d'une nouvelle espèce nominale qu'un spécimen, et un spécimen seulement, est « le type » ou emploie une expression équivalente », ce spécimen est l'holotype ». (Article 73 a et b).

Syntypes ; « Si une nouvelle espèce nominale n'a pas d'holotype... tous les spécimens de la série-type sont des « syntypes », d'une valeur égale en nomenclature ». (Article 73 c).

Quelques-unes des espèces décrites par Cuvier sont fondées sur un holotype unique ou sur une série de syntypes. D'autres sont fondées sur le dessin ou les descriptions d'observateurs antérieurs ; le type est alors le spécimen illustré ou décrit par l'auteur original. Dans plusieurs cas, Bauchot et Blanc ont considéré les descriptions de Lacépède (1800, 1802) et Cuvier (1817, 1829) comme *nomina nuda*. Il est maintenant nécessaire d'appliquer les articles 12 et 16 du Code, qui précisent que les descriptions d'espèces, antérieures à 1931, sont valables quand elles se réfèrent à une figure, ou une description d'une publication antérieure, parce que cette référence bibliographique constitue une « indication ». Donc, les spécimens examinés par Cuvier et Valenciennes (1831) pour compléter les descriptions antérieures dans l'*Histoire Naturelle des Poissons*, ne sont pas des types.

Néotype : « Un néotype ne doit être désigné que dans le cadre d'un travail de révision, et seulement dans des circonstances exceptionnelles, lorsqu'une telle désignation est nécessaire au maintien de la stabilité de la nomenclature » (Article 75 a). Aucun des néotypes ou néosyntypes désignés par Bauchot et Blanc ne remplissent les conditions du Code International.

En accord avec Fraser-Brunner (1950), Collette et Gibbs (1963), et autres auteurs, la famille des Scombridae groupe les familles des Cybiidae, Sardidae, Thunnidae et Katsuwonidae. Les espèces citées par Bauchot et Blanc sont mentionnées ici suivant l'ordre phylogénétique établi par Collette et Gibbs (1963).

Après mention de la description originale, l'indication précise du statut actuel de chaque espèce nominale suit le signe =. La longueur à la fourche (FL) est donnée de préférence à la longueur standard ou à la longueur totale, parce que cette mensuration est l'indication de taille la plus commode et la plus communément utilisée chez les Scombridae. Les caractères utiles à l'identification des espèces nominales, tels que nombre de vertèbres, de rayons des nageoires, de branchiospines, sont donnés pour la plupart des types.

J'exprime ma profonde gratitude à M^{me} M. L. Bauchot qui m'a aidé durant mon séjour au Muséum de Paris, m'a fourni les radiographies d'un grand nombre de types, et a traduit en français la plus grande partie de ce travail. M. T. Matsui m'a aimablement fait part de ses études encore non publiées sur *Scomber* et *Rastrelliger*. Les D^{rs} R. H. Gibbd, Jr., et D. M. Cohen ont lu et critiqué ce manuscrit.

Genre **Scomber** Linnaeus, 1758.

Scomber antarcticus F. de Castelnau, 1872, Proc. Zool. Acclimat. Soc. Victoria, t. I, p. 106.

= *Scomber australasicus* Cuvier.

Holotype — B. 2125 : Marché de Melbourne, F. de Castelnau.
Sec, en herbier, assez mauvais état.
Fig. 22, Blanc et Bauchot (1964).
FL : 296 mm.

Remarques. — Pour Fraser-Brunner (1950) et Bauchot et Blanc *S. antarcticus* est synonyme de *S. japonicus*. Whitley (1964) met ce nom en synonymie avec l'espèce australienne commune *S. australasicus*.

Scomber pneumatophorus Delaroche 1809, Ann. Mus. Hist. Nat. Paris, t. XIII, p. 334.

= *Scomber japonicus* Houttuyn.

Holotype — A. 5284 : Iviça (I. Baléares), Delaroche.

Alcool, bon état.

Fig. 28, Blanc et Bauchot (1964).
FL : 180 mm.
Vertèbres : 14 + 17 = 31.
Branchiospines : 10 + 31 = 41.
Interneuraux sous la première dorsale : 14.
Dents fortement développées sur les palatins mais absentes sur le vomer. Épine anale courte, forte, séparée de la nageoire anale.
Hauteur maximum du corps : 10 % FL.

Scomber capensis Cuvier *in* Cuvier et Valenciennes, 1831, Hist. Nat. Poiss., t. VIII, p. 56.

= *Scomber japonicus* (Houttuyn).

D'après Bauchot et Blanc (1961, p. 374) « L'espèce nouvelle établie d'après un squelette préparé par Delalande, et originaire du Cap de Bonne Espérance, n'a pas été retrouvée dans nos collections ».

Scomber australasicus Cuvier *in* Cuvier et Valenciennes, 1831, Hist. Nat. Poiss., t. VIII, p. 49.

= *Scomber australasicus* Cuvier.

Holotype — A. 5312 : Port du Roi Georges (Australie S. W.), Quoy et Gaimard (1829, Voy. « Astrolabe »).

Alcool, mauvais état.

Fig. 23, Blanc et Bauchot (1964).
FL : 187 mm.
Vertèbres : 14 + 17 = 31.
Branchiospines : 13 + 25 = 38.
Interneuraux sous la première dorsale : 19.
Dents bien développées sur le vomer et les palatins. Épine anale courte, forte, séparée de la nageoire anale.
Hauteur maximum du corps : 15 % FL.

Remarques. — Pour Fraser-Brunner (1950) et Bauchot et Blanc *S. australasicus* est synonyme de *S. japonicus*. Pour Whitley (1964) c'est une espèce valide. *S. australasicus* se rapproche des espèces de *Scomber* et diffère des espèces de *Rastrelliger* par la possession d'une courte épine anale libre et la présence de dents bien développées sur les palatins et le vomer. Elle diffère de *S. japonicus* par un plus grand nombre d'interneuraux sous la première nageoire dorsale.

Genre **Rastrelliger** Jordan et Starks, 1908.

Scomber kanagurta Cuvier, 1817, Règne animal, t. II, p. 313.

= *Rastrelliger kanagurta* (Cuvier).

Remarques. — Bauchot et Blanc considèrent comme syntypes les spécimens cités par Cuvier (1831) dans sa description pour l'*Histoire Naturelle des Poissons*. En fait, la description originale, dans la première édition du *Règne animal*, était fondée sur un spécimen du Vizagapatam, India, figuré par Russell (1803, fig. 136). Ainsi, les cinq spécimens cités par Bauchot et Blanc n'ont pas valeur de type.

Scomber loo Lesson 1829, Dict. class. d'hist. nat., t. 15, p. 277.

= *Rastrelliger kanagurta* (Cuvier).

Holotype — 2910 : Port Praslin, I. Nouvelle-Irlande (Mélanésie), Lesson et Garnot (Voy. « La Coquille », 1822-25).

Alcool, très mauvais état.
Fig. 27, Blanc et Bauchot (1962).
FL : 231 mm.
Vertèbres : 13 + 18 = 31.
Branchiospines : 22 + 41 = 63.
Inerneuraux sous la première dorsale : 11.
Vomer et palatins sans dents.
Hauteur maximum du corps : 22 % FL.
Longueur de la tête plus grande que la hauteur maximum du corps : 28 % FL.

Genre **Scomberomorus** Lacépède, 1802.

Cybium cavalla Cuvier, 1829, Règne animal, 2e édit., t. II, p. 200.

= *Scomberomorus cavalla* (Cuvier).

Remarques. — Cuvier (1829) crée *C. cavalla* d'après la description et le dessin du « Guarapucu » de Marcgrave (1648, p. 179) ; ainsi les quatre spécimens cités par Bauchot et Blanc ne sont pas des types.

Cybium acervum Cuvier *in* Cuvier et Valenciennes, 1831, Hist. Nat. Poiss., t. VIII, p. 186.

= *Scomberomorus cavalla* (Cuvier).

Lectotype — A. 5781 : Saint-Domingue, Ricord.

Alcool, assez bon état.
FL : 130 mm.
Vertèbres : 17 + 25 = 42.

Branchiospines : 1 + 1 + 7 = 9
Dorsale : XV + 17 + VIII.
Anale : 18 + VIII.

Paralectotypes — B. 2508 (extrait de A. 5781 Catalogue Bauchot-Blanc) : Saint-Domingue, Ricord.

Alcool, assez bon état.

FL : 133, 138 mm.
Vertèbres : 17 + 25 = 42.
Branchiospines : 1 + 1 + 8 = 10 ; 2 + 1 + 7 = 10.
Dorsale : XV + 18 + VIII ; XV + 17 + VII.
Anale : 20 + VIII ; 19 + VIII.

Remarques. — Pour Fraser-Brunner (1950) Rivas (1951) et Bauchot et Blanc *Cybium acervum* est synonyme de *Scomberomorus regalis* (Bloch). Le plus petit des quatre syntypes (A. 5782, Martinique, Achard, 113 mm FL) a 3 + 1 + 12 = 16 branchiospines, 20 + 28 = vertèbres, valeurs caractéristiques de *S. regalis* (Mago Leccia, 1958). Mais les trois plus grands syntypes sont des *S. cavalla*. De plus, la description originale indique : « Ses dents sont tranchantes, comme dans le *regale*, mais moins nombreuses ; je n'en compte que huit ou neuf à la mâchoire supérieure, et sept ou huit à l'inférieure ». A. 5782 a 11-13 dents à la mâchoire supérieure et 10-12 à la mâchoire inférieure ; les spécimens B. 2508 et A. 5781 ont 6-11 à la mâchoire supérieure et 7-8 à la mâchoire inférieure. Le spécimen désigné ici comme lectotype a 8 dents sur un côté de la mâchoire supérieure et 11 sur l'autre ; 7 sur un côté de la mâchoire inférieure et 8 sur l'autre.

Cybium immaculatum Cuvier *in* Cuvier et Valenciennes, 1831, Hist. Nat. Poiss., t. VIII, p. 191.

= *Scomberomorus cavalla* Cuvier.

Lectotype — A. 5720 : Martinique Plée.

Alcool, mauvais état.

Spécimen avec étiquette métallique.
FL : 157 mm.
Vertèbres : 17 + 25 = 42.
Branchiospines : 1 + 1 + 7 = 9.
Dorsale : XV + 17 + IX.
Anale : 17 + IX.

Paralectotypes — B. 2509 (extrait de A. 5720 Catalogue Bauchot-Blanc) : Martinique, Plée.

Alcool, mauvais état.

FL : 147 mm.
Vertèbres : 17 + 24 = 41.
Branchiospines : 1 + 1 + 6 = 8.
Dorsale : XV + 17 + IX.
Anale : 18 + VIII.

A. 5780 : Martinique, Plée.
Alcool, très mauvais état.
FL : 164 mm.
Vertèbres : 17 + 25 = 42.
Branchiospines : 1 + 1 + 7 = 9.
Dorsale : XV + 17 + IX.
Anale : 19 + VIII.

Remarques. — Fraser-Brunner (1950), Rivas (1951) et Bauchot et Blanc s'accordent tous à penser que *C. immaculatum* est synonyme de *C. cavalla*. Aucune localité n'est mentionnée dans la description originale mais le catalogue a autorisé Bauchot et Blanc à préciser que A. 5720 et A. 5780 sont syntypes. Le plus grand des deux spécimens enregistré A. 5720 est désigné ici comme lectotype parce qu'il se rapproche le plus de la description originale de Cuvier, par le nombre des rayons des nageoires ; c'est le seul qui ait neuf pinnules. Il est également en meilleur état de conservation que A. 5780.

Cybium tritor Cuvier *in* Cuvier et Valenciennes, 1831, Hist. Nat. Poiss., t. VIII, p. 176, pl. 218.

= *Scomberomorus tritor* (Cuvier).

Holotype — A. 6871 : Gorée, Rang.
Alcool, assez bon état.
Fig. 19, Blanc et Bauchot (1962).
FL : 658 mm.
Branchiospines : 2 + 1 + 10 = 13.
Dorsale : XV + 17 + VIII.
Anale : 17 + VIII.

Paratype — A. 6868 : Gorée, Rang.
Alcool, assez bon état.
Fig. 20, Blanc et Bauchot (1962).
FL : 505 mm.
Branchiospines : 3 + 1 + 11 = 15.
Dorsale : XV + 17 + VIII.
Anale : 17 + IX.

Scomber regalis Bloch, 1793, Naturg. Ausländ. Fische, t. X, p. 38, pl. 333.

= *Scomberomorus regalis* (Bloch).

Remarques. — Bauchot et Blanc n'ont pas justifié la désignation comme « néosyntypes » de *Scomber regalis* Bloch, de deux exemplaires examinés par Cuvier (1831). Pour cette raison ces exemplaires n'ont aucune valeur de types.

Cybium lineolatum Cuvier *in* Cuvier et Valenciennes, 1831, Hist. Nat. Poiss., t. VIII, p. 170.

= *Scomberomorus lineolatus* (Cuvier).

Holotype — A. 6866 : Malabar, Dussumier.

Alcool, bon état.
Fig. 15, Blanc et Bauchot (1962).
FL : 707 mm.
Branchiospines : 1 + 1 + 8 = 10.
Dorsale : environ XVI + 16 + IX.
Anale : 16 + X.

Paratype — 6357 : Mahé, Bélenger.
Alcool, très mauvais état (tête et caudale restent seules).
Fig. 16, Blanc et Bauchot (1962).

Remarques. — Il est clair que la description originale de Cuvier est fondée sur le spécimen A. 6866, que Bauchot et Blanc considèrent comme holotype. Le spécimen envoyé par Bélenger est rapporté avec réserve à *Cybium lineolatum*, si bien qu'il serait bon de ne pas le considérer comme type. D'après Williams (1960) *Scomberomorus lineolatus* est une espèce valide, non synonyme de *S. guttatus* Bloch et Schneider comme l'a considéré Fraser-Brunner (1950).

Cybium interruptum Cuvier *in* Cuvier et Valenciennes, 1831, Hist. Nat. Poiss., t. VIII, p. 172.

= *Scomberomorus lineolatus* Cuvier.

Holotype — A. 5522 : Pondichéry, Leschenault.
Sec, assez bon état mais la dorsale est en mauvais état.
Fig. 13, Blanc et Bauchot (1962).
FL : 375 mm.

Remarques. — D'après Williams (1960) *Cybium interruptum* est synonyme de *Scomberomorus lineolatum.*

Cybium kuhlii Cuvier *in* Cuvier et Valenciennes, 1831, Hist. Nat. Poiss., t. VIII, p. 178.

= *Scomberomorus guttatus* (Bloch et Schneider).

Lectotype — A. 5771 : Java, Kuhl et Van Hasselt.
Alcool, bon état.
Fig. 14, en haut, Blanc et Bauchot (1962).
FL : 107,5 mm.
Vertèbres : 21 + 30 = 51.
Branchiospines : 2 + 1 + 9 = 12.
Dorsale : XVII + 21 + VIII.
Anale : 21 + VIII.

Paralectotype — A. 5715 : Bombay, Dussumier.
Alcool, bon état.
Fig. 4, en bas, Blanc et Bauchot (1962).
FL : 114,5 mm.

Vertèbres : 21 + 29 = 50.
Branchiospines : 2 + 1 + 8 = 11.
Dorsale : XVII + 22 + VIII.
Anale : 22 + VII.

Remarques. — Pour De Beaufort (1951) et Silas (1964) *Cybium kuhlii* est synonyme de *Scomberomorus guttatus*. Bauchot et Blanc identifient A. 5771 comme holotype et A. 5715 comme paratype, mais aucun spécimen n'est désigné comme type dans la description originale. Cette dernière est fondée en premier lieu sur A. 5771, aussi ce spécimen est-il désigné ici comme lectotype.

Scomber commerson Lacépède, 1802, Hist. Nat. Poiss., t. II, p. 598, pl. XX.

= *Scomberomorus commerson* (Lacépède).

Remarques. — Lacépède fit la description de cette espèce d'après un manuscrit de Commerson. Bauchot et Blanc considèrent comme « néosyntypes » les quatre spécimens utilisés par Cuvier pour redécrire cette espèce. Aucune justification n'a été donnée pour désigner un néotype et le Code international de Nomenclature ne prévoit pas de « néosyntypes ».

Cybium clupeoidum Cuvier *in* Cuvier et Valenciennes, 1831, Hist. Nat. Poiss., t. VIII, p. 178.

= *Scomberomorus commerson* (Lacépède).

Holotype — A. 5784 : Ile de Norfolk (ouest de l'Australie), collection Broussonet.

Alcool, assez bon état.
Fig. 3, Blanc et Bauchot (1962).
FL : 302 mm.
Vertèbres : 17 + 25 = 42.
Branchiospines : 1 + 1 + 7 = 9.
Dorsale : XV + 17 + IX.
Anale : 18 + VIII.

Ligne latérale haute antérieurement, s'infléchissant rapidement sous la deuxième dorsale, et se prolongeant postérieurement avec de légères ondulations.

Remarques. — Munro (1943) retient *Cybium clupeoidum* comme espèce douteuse. Bauchot et Blanc l'ont considérée comme synonyme de l'espèce ouest-atlantique *S. cavalla*. Le nombre relativement faible de vertèbres et de branchiospines, ainsi que l'infléchissement de la ligne latérale sous la seconde dorsale indiquent que *clupeoidum* est synonyme de l'espèce indo-pacifique à large distribution *S. commerson*.

Genre **Orcynopsis** Gill, 1862.

Cybium altipinne Guichenot *in* Duméril. 1861, Arch. Mus. Hist. Nat. Paris, t. X, p. 269.

= *Orcynopsis unicolor* (Geoffroy St Hilaire).

Holotype — A. 5797 : Sénégal, Heudelot.

Alcool, bon état.

Fig. 2, Blanc et Bauchot (1962).
FL : 405 mm.
Vertèbres : 19 + 19 = 38.
Branchiospines : 3 + 1 + 11 = 15.
Dorsale : XIV + 14 + VIII.
Anale : 14 + VII.
Palatins et vomer avec groupes de dents.
Langue avec deux groupes de dents.

Remarques. — Plusieurs auteurs comme Fraser-Brunner (1950) et Baúchot et Blanc considèrent *Cybium altipinne* comme synonyme de *Scomberomorus tritor*. Le petit nombre de vertèbres, les deux groupes de dents linguales et l'absence d'échancrure dans la plaque hypurale montrent que *C. altipinne* est synonyme de *Orcynopsis unicolor*.

Genre **Sarda** Cuvier, 1829.

Pelamys chiliensis Cuvier *in* Cuvier et Valenciennes, 1831, Hist. Nat. Poiss., t. VIII, p. 163.

= *Sarda chiliensis* (Cuvier).

Holotype — A. 5608 : Valparaiso, D'Orbigny.

Sec, bon état.

Fig. 21, Blanc et Bauchot (1962).
FL : 672 mm.
Dorsale : XVIII + 13 + VIII.
Anale : 12 + VI.
Pectorale : 24.
Dents à la mâchoire inférieure : 16 + 19.

Thynnus brachypterus Cuvier, 1879, Règne animal, 2e édit., t. II, p. 198.

= *Sarda sarda* (Bloch).

Remarques. — Plusieurs auteurs comme Fraser-Brunner (1950), Rivas (1951) et Bauchot et Blanc considèrent *Thynnus brachypterus* comme synonyme de *Thunnus thynnus*. Cette espèce est établie d'après la « pelamyde vera » de Rondelet (1554, p. 245) et la fig. 5, pl. VII de Duhamel du Monceau (1769). Les figures sont très difficiles à identifier mais le profil régulièrement infléchi de la première nageoire dorsale, l'absence de lobes dorsal et anal, et les bandes verticales indiquent que *T. brachypterus* est le jeune de *Sarda sarda.*

Les spécimens utilisés par Cuvier pour la redescription en 1831, et désignés par Bauchot et Blanc comme syntypes, n'ont aucune valeur de types. Quatre de ces spécimens (A. 5299, A. 5377, A. 5791) sont *Thynnus thynnus* et le cinquième (A. 5316) est *Euthynnus alletteratus.*

Genre **Auxis** Cuvier, 1829.

Auxis vulgaris Cuvier *in* Cuvier et Valenciennes, 1831, Hist. Nat. Poiss., t. VIII, p. 139.

= *Auxis rochei* (Risso).

Syntype — A. 5808 : Nice, Laurillard.

Syntype — A. 5815 : Morée, Bory St. Vincent.

Syntype — A. 5742 : Martinique, Plée.

Remarques. — Bauchot et Blanc écrivent qu'aucun des types d'*Auxis*, bien qu'inscrits dans les registres, n'a été retrouvé dans les collections en dépit de longues recherches. Pour un grand nombre d'auteurs, les dix espèces nominales d'*Auxis* représentent une seule espèce à répartition mondiale. Récemment plusieurs auteurs ont démontré l'existence de deux espèces, au moins dans l'Océan Pacifique. Fitch et Roedel (1963) mentionnent une seule espèce atlantique pour laquelle ils recommandent d'utiliser le nom *Auxis rochei.*

Auxis Ramsayi Castelnau 1879, Proc. Linn. Soc. New South Wales, t. 3, pt. 4, p. 382.

= *Auxis rochei* (Risso).

Holotype — A. 1241 : acheté au marché de Sydney le 6 avril 1878 et entré dans les collections en 1879, De Castelnau.

Remarques. — Le type de *Auxis Ramsayi* est également perdu, d'après Bauchot et Blanc. Whitley (1964) a, avec exactitude semble-t-il, considéré *A. Ramsayi* comme synonyme de l'*Auxis* à large corselet qu'il a appelé *A. thynnoides* Bleeker mais qui selon Fitch et Roedel (1963) serait *A. rochei.*

Genre **Euthynnus** Lütken, 1882.

Thynnus thunnina Cuvier, 1829, Règne animal, 2e édit., t. II, p. 198.

= *Euthynnus alletteratus* (Rafinesque).

Remarques. — Cette espèce est établie d'après la pl. 24, fig. 5 d'Aldrovandi (1613) ; pour cette raison « l'holotype » désigné par Bauchot et Blanc d'après la redescription de Cuvier (1831) n'a pas valeur de type.

Thynnus brasiliensis Cuvier *in* Cuvier et Valenciennes, 1831, Hist. Nat. Poiss., t. VIII, p. 110.

= *Euthynnus alletteratus* (Rafinesque).

Holotype — A. 5571 : Brésil, Delalande.

Sec, assez bon état.

Fig. 34, Blanc et Bauchot (1962).
FL : 695 mm.
Pectorale : 28.

Thynnus brevipinnis Cuvier *in* Cuvier et Valenciennes, 1831, Hist. Nat. Poiss., t. VIII, p. 112, pl. 216.

= *Euthynnus alletteratus* (Rafinesque).

Holotype — A. 5810 : Naples, Savigny.

Alcool, assez bon état.

Fig. 35, Blanc et Bauchot (1962).
FL : 324 mm.
Branchiospines : 11 + 28 = 39.
Dorsale : XVII + 12 + VIII.
Anale : 13 + VII.
Pectorale : 28.

Remarques. — La description originale n'indique comme provenance que « Méditerranée » mais les catalogues ont permis à Bauchot et Blanc d'identifier A. 5810 comme holotype.

Genre **Thunnus** South, 1845.

Thynnus coretta Cuvier *in* Cuvier et Valenciennes, 1831, Hist. Nat. Poiss., t. VIII, pl. 102.

= *Thunnus atlanticus* (Lesson).

Holotype — A. 5380 : Martinique, Plée.

Alcool, bon état.

Fig. 36, Blanc et Bauchot (1962).
FL : 263 mm.
Vertèbres : 19 + 20 = 39.
Branchiospines : 7 + 17 = 24.
Pectorale : 32.

Remarques. — Cuvier utilisa le premier le nom *T. coretta* pour *Scomber major torosus* de Sloane (1701, pl. I, fig. 3) en 1829. Le nom est établi d'après la planche, aussi n'est-il pas un *nomen nudum* comme l'ont pensé Bauchot et Blanc. Cependant, la figure n'est pas identifiable (Gibbs et Collette, sous presse), aussi le nom doit-il être regardé comme un *nomen dubium*. La description de *T. coretta* en 1831 est faite d'après A. 5380. Le nombre vertébral de 19 + 20 (au lieu de 18 + 21) et le faible nombre de branchiospines prouvent que ce spécimen est *T. atlanticus* et non *T. thynnus* comme l'ont indiqué BAUCHOT et BLANC.

Thynnus pacificus Cuvier *in* Cuvier et Valenciennes, 1831, Hist. Nat. Poiss., t. VIII, p. 133.

= *Thunnus alalunga* (Bonnaterre).

REMARQUES. — BAUCHOT et BLANC indiquent A. 6862, Mer des Indes, DUSSUMIER, comme holotype de *Thynnus pacificus*. L'appellation *T. pacificus* est un nom de remplacement pour *Scomber germo* Lacépède (1800) établi d'après un spécimen de l'Océan Pacifique décrit dans les manuscrits de COMMERSON.

Thynnus argentivittatus Cuvier *in* Cuvier et Valenciennes, 1831, Hist. Nat. Poiss., t. VIII, p. 134.

= *Thunnus albacares* (Bonnaterre) ?

Syntype — A. 5567 : Mer des Indes, DUSSUMIER.
Sec, mauvais état.
Fig. 30, BLANC et BAUCHOT (1962).
FL : 457 mm.

Syntype — A. 5572 : Atlantique, QUOY et GAIMARD.
Sec, mauvais état.
Fig. 29, BLANC et BAUCHOT (1962).
FL : 615 mm.

REMARQUES. — La description originale est fondée sur les deux seuls syntypes cités ci-dessus. SCHAEFER et WALDORF (1950) ont cru qu'il y avait trois syntypes et, à tort, ont désigné comme lectotype de *Thynnus argentivittatus* le spécimen A. 5814 envoyé de la côte de Malabar par DUSSUMIER (et mentionné dans leur publication sous le numéro erroné A. 5168) (BLANC et BAUCHOT, 1962). SCHAEFER et WALFORD ont alors utilisé *Thunnus argentivittatus* pour les populations de *Thunnus albacares* de l'Océan Indien. RIVAS (1961) utilise *argentivittatus* pour un thon de l'Océan Indien qu'il place dans le sous-genre *Parathunnus*. Le lectotype supposé, A. 5814, est un spécimen de *Thunnus tonggol* (Bleeker).

L'identité des deux vrais syntypes est une autre question. Au cours de la révision systématique et anatomique des thons du genre *Thunnus* (GIBBS et COLLETTE, sous presse), le Dr. GIBBS et moi-même avons examiné les syntypes mais nous avons été incapables de justifier le choix de l'un d'eux comme lectotype. Les valeurs métriques ne prouvent pas que ces syntypes appartiennent à l'espèce *T. albacares*. La distance du museau à l'origine de la seconde dorsale semble éliminer l'identification à *T. thynnus*, *T. alalunga* et *T. obesus*. Mais il reste encore *T. atlanticus* et *T. tonggol*. Le choix du spécimen atlantique éliminerait l'espèce indo-pacifique *T. tonggol* et le choix du spécimen de l'Océan Indien éliminerait *T. atlanticus*.

SUMMARY.

Reexamination of the type material of Scombridae in the collections of the Museum de Paris has disclosed that a number of changes are necessary in the *Catalogue des types de Scombroidei* by BAUCHOT and BLANC (1961), and also BLANC and BAUCHOT (1962). The purpose of this paper is to determine the status and identity of these scombrid types.

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PROPOSED SUPPRESSION OF THREE *NOMINA OBLITA* IN THE FAMILY BELONIDAE (PISCES). Z.N.(S.) 1723

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Revisionary studies on the family Belonidae for the "Fishes of the Western North Atlantic" necessitate the resolution of several conflicts in nomenclature between the recent papers by Berry and Rivas (1962) and Mees (1962, 1964). The purpose of this application is to request the International Commission on Zoological Nomenclature to suppress three *nomina oblita* used by Mees (1962, 1964) in contradiction to the provisions of Article 23b of the International Code of Zoological Nomenclature. More detailed discussion on the above papers is given elsewhere (Collette and Berry, 1965).

I. *Strongylura marina* (Walbaum)

The name *Esox marinus* Walbaum, 1792, has been consistently used to refer to this common western Atlantic needlefish, either as *Tylosurus marinus* or as *Strongylura marina* (Jordan and Fordice, 1887 : 351; Jordan and Evermann, 1896 : 714; Fowler, 1919 : 5; Hildebrand and Schroeder, 1928 : 148; Jordan, Evermann, and Clark, 1930 : 196; Breder, 1932 : 6; Bigelow and Schroeder, 1953 : 167; American Fisheries Society Checklist, 1960 : 20; Berry and Rivas, 1962 : 155). Mees (1962 : 33–36) resurrected the name *Esox houttuyni* which was described by Walbaum on the same page (p. 88) of the same paper in which he described *marinus*. Mees admitted that ". . . *marinus* has been widely used, whereas I am not aware that anybody has ever used the name *houttuyni* subsequent to its appearance in literature. This, however, I do not consider a drawback. . . ." We have not been able to find any reference to Walbaum's *houttuyni* other than the two given by Mees, the original description and a listing by Bloch and Schneider (1801 : 391) as "Var. b. *Houttuyni*" under *Esox belone*.

Therefore, under the provisions of Article 23b of the International Code, we request the International Commission to:

(1) place the specific name *houttuyni* Walbaum, 1792, as published in the binomen *Esox houttuyni* on the Official Index of Rejected and Invalid Specific Names in Zoology;

(2) place the specific name *marinus* Walbaum, 1792, as published in the binomen *Esox marinus* on the Official List of Specific Names in Zoology.

II. *Tylosurus crocodilus* (Peron and LeSueur)

In the western Atlantic Ocean, one species of needlefish has consistently been known as *Strongylura* or *Tylosurus raphidoma* (Ranzani, 1842) since about 1887 (Jordan and Fordice, 1887 : 353; Jordan and Evermann, 1896 : 715; Fowler, 1919 : 5; Jordan, Evermann, and Clark, 1930 : 196; Breder, 1932 : 14;

American Fisheries Society Checklist, 1960 : 20; Berry and Rivas, 1962 : 155). Mees (1962) regarded this species as worldwide and as having been described earlier in other parts of the world. The two most often used senior synonyms of *raphidoma*, on this systematic judgement, are *Belona crocodila* Peron and LeSueur, in LeSueur, 1821 (type locality Mauritius) and *Belone choram* Rüppell, 1837 (type locality Red Sea). Rüppell's name was based on Forskål (1775 : 67). After pointing this out, Mees (1962 : 45) continued: "This does not mean, however, that I agree with Weber & de Beaufort and with all other modern authors, that now *Belona crocodila* LeSueur (1821) becomes the oldest name available for the species, for Bloch & Schneider (1801) already based a name on Forskål's description, and their name *Marisrubri*, which apparently has not been used since its introduction, is the oldest name available." The closest approach we have found to the use of the name *marisrubri* for a needlefish, prior to Mees, was Valenciennes' use (in Cuvier and Valenciennes, 1846 : 328) of "de la phrase de Forskal . . . *Esox belone maris rubri*" in referring to Forskål's original paper.

Peron and LeSueur's description of *Belona crocodila* fits this species adequately and this specified name has been widely used throughout the Indo-West Pacific: Valenciennes *in* Cuvier and Valenciennes, 1846 : 327; Weber and de Beaufort, 1922 : 128; Fowler, 1928 : 74; Herre, 1928 : 229; Herre, 1953 : 448; Munro, 1955 : 72; Fowler, 1956 : 139; Smith, 1961 : 130. Some authors have also used the name for the population in the eastern Atlantic (Fowler, 1936 : 445; Poll, 1953 : 168).

Therefore, we request that the International Commission take action under the provisions of Article 23b of the International Code to:

(1) place the subspecific name *Maris rubri* Bloch and Schneider, 1801, as published in the trinomen *Esox belone* Var. *Maris rubri*, on the Official Index of Rejected and Invalid Specific Names in Zoology;

(2) place the specific name *crocodila* Peron and LeSueur, *in* LeSueur, 1821, as published in the binomen *Belona crocodila*, on the Official List of Specific Names in Zoology.

III. *Tylosurus acus* (Lacépède)

The third species of needlefish has had a more complicated nomenclatorial history than the preceding two. At least eight names have been used for it in the Atlantic, and three more names were established for its Indo-Pacific representatives. Günther (1866 : 241–242) recognized *Belona carribaea* LeSueur, 1821, and *Tylosurus cantrainii* Cocco, 1833, but did not mention *Sphyraena acus* Lacépède, 1803, or *Esox imperialis* Rafinesque, 1810. In their review of the American species of Belonidae, Jordan and Fordice (1887 : 355) recognized *acus* and tentatively placed *imperialis* and *cantrainii* in its synonymy. They also recognized *carribaea*, but stated that it was very close to and might be the same as *acus*. Jordan and Evermann (1896 : 716–717) and Jordan, Evermann, and Clark (1930 : 197) also recognized both *acus* and *carribaea*. Following Jordan's concepts, most publications on Atlantic Belonidae refer only to the name *acus* (Fowler, 1919 : 5; Hildebrand and Schroeder, 1928 : 149; Breder, 1932: 14; Fowler, 1936 : 443; American Fisheries Society Checklist, 1960 : 20). Fowler questioningly (1944 : 81) placed *acus* in the synonymy of *carribaea*. Berry and Rivas (1962 : 155) placed *carribaea* in the synonymy of *acus* and did not refer to the eastern Atlantic *imperialis* and *cantrainii*.

The original description (p. 325) and figure (pl. 1, fig. 3) of *Sphyraena acus* Lacépède, 1803, refer to one of the two species of *Tylosurus* in the Atlantic. The counts of 25 dorsal and 24 anal rays are at the upper limit of the counts we have made (dorsal 23–26, mode 24; anal 20–24; mode 22) for the species presently known as *acus*, and the anal ray count is two rays higher than the maximum we have found for *Tylosurus crocodilus*. If the fin ray counts are accepted, the only other species of needlefish that could have been represented is *Ablennes hians* (Valenciennes, 1846); Lacépède's figure, although crudely drawn, clearly is not *hians*, because it lacks the falcate pectoral fin, the arched based on the upper jaw, dark body bars, and the compressed body of *hians*. Based on the fin ray counts and the figure of Lacépède, there is little doubt that Jordan and Fordice (1887) were justified in considering the description of *acus* to be identifiable with this species.

After rejecting the poorly described *acus*, Mees (1962 : 38–40) chose to recognize the equally poorly described *Esox imperialis* Rafinesque, 1810. Mees admitted that the number of dorsal and anal rays in the original description was higher than that for any needlefish (except the South American freshwater genus *Potamorrhaphis*). However, he felt justified because the description appeared to be of a needlefish different from the common Mediterranean *Belone belone* and so must refer to the only other species of Mediterranean needlefish. This argument is not valid because we have examined a third species of needlefish from the Mediterranean – *Tylosurus crocodilus*. Furthermore, a large proportion of the museum specimens of *Belone belone* and *Tylosurus acus* that we have examined have been misidentified, so we see no reason to assume that Rafinesque necessarily distinguished between them.

If *acus* were rejected as unidentifiable, then *imperialis* would similarly be rejected, and the name *carribaea* LeSueur, 1821, would then be available. This would be another reasonable solution, especially because the number of fin rays in LeSueur's original description (dorsal 24, anal 22) matches the mode for the western Atlantic specimens we have examined. Also, LeSueur contrasted the slender jaws and elongated body of *carribaea* with the stout jaws and thick body of *crocodila*, indicating that he had both species. However, in view of the wide usage that *acus* has had up until the time of Mees (1962, 1964), it seems in the best interests of stability to retain it. The name *imperialis* has apparently not been used as a senior synonym since its original description, except by Mees (1962, 1964) and by Tortonese (1963).

Therefore, under the provisions of Article 23b of the International Code, we request the International Commission to:

(1) place the specific name *imperialis* Rafinesque, 1810, as published in the binomen *Esox Imperialis* on the Official Index of Rejected and Invalid Specific Names in Zoology;

(2) place the specific name *acus* Lacépède, 1803, as published in the binomen *Sphyraena acus* on the Official List of Specific Names in Zoology.

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REARING PENAEID SHRIMP FROM EGGS TO POSTLARVAE[1]

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ABSTRACT

A description is given of the physical facilities in which mass cultures of penaeids have been reared from eggs to postlarvae. The metal chelator EDTA was added to the water in which the shrimp were grown. Larvae of *Penaeus aztecus* developed more rapidly at 30° C than at lower temperatures. Salinity varied from 20.5% to 36.0% during rearing trials in which *P. aztecus* larvae were reared to postlarvae. Addition of mixed algal cultures as food gave better survival than additions of their individual components. EDTA was used as an additive to filtered sea water to grow a diatom, *Skeletonema* sp., in mass culture, as food for larval shrimp.

INTRODUCTION

The shrimp fishery, the most valuable fishery in the United States, has been characterized by wide annual fluctuations in the commercial catch. Biologists at the Bureau of Commercial Fisheries Biological Laboratory at Galveston, Texas, are studying the life histories of the commercially important shrimps in an attempt to discover the causes of the fluctuations. These shrimp spend their adult life in offshore waters, where they reach sexual maturity and spawn. After a short planktonic existence, during which the eggs hatch and the larval stages are completed, the shrimp enter the estuaries as small postlarvae. After several months of rapid growth in the estuaries, the young shrimp migrate back to the offshore waters.

Investigations during the past five years indicate that the numbers of postlarval brown shrimp, *Penaeus aztecus*, entering Galveston Bay nurseries can be closely correlated with the annual commercial catch (Baxter, 1962 and Baxter et al., 1965). Apparently mortalities in this estuary are not of sufficient magnitude to account for the yearly fluctuations. The fluctuations also do not seem to be caused by a lack of spawning shrimp. It would appear then, that the most critical factors are those affecting survival of the larvae or early postlarvae while they are still offshore.

One of the prerequisites in attempts to delineate these factors is precise identification of larvae taken in plankton samples. The most reliable method of obtaining accurate identifications of larvae is to rear them under controlled conditions from eggs of known parentage. Sufficient criteria have been established so that the three species of commercially important shrimp of the genus *Penaeus* can be separated from other species in the samples. They cannot, however, be distinguished from each other. Both pink shrimp (*P. duorarum*) and brown shrimp have been reared in the laboratory and complete larval series have been obtained with which detailed taxonomic studies are being conducted. Larvae of white shrimp (*P. setiferus*) of known parentage are not yet available.

We have experienced some success in rearing shrimp but are still trying to modify procedures so that sufficient numbers of larvae can be grown in mass culture to supply material for detailed physiological studies. If physiological requirements of larvae can be determined in the laboratory, personnel engaged in field studies will have a better idea of which environmental factors to measure.

The Japanese have cultured penaeid larvae for years (Hudinaga, 1942), but, with a few exceptions, attempts in this country and elsewhere have been unsuccessful. Heldt (1938) and Ewald (1965) succeeded in rearing small numbers of larvae to postlarvae. Johnson and Fielding (1956) reared large numbers in ponds, but unfortunately their work has not been duplicated.

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We have successfully reared four species (brown; pink; seabob, *Xiphopeneus krøyeri*; and *Trachypeneus similis*) in small mass cultures. During our studies, we have developed rearing techniques and made observations on larval growth and behavior that are presented here.

CULTURE METHODS

Ripe female shrimp are caught in commercial, 45-foot, otter trawls. It is generally not necessary to take males because females are implanted with a spermatophore at sea, and the eggs are fertilized as they are spawned. In most species of penaeid shrimp, the spermatophore is placed internally and is lost only when the exoskeleton is shed, but in some species, including the white shrimp, it is placed externally and is usually dislodged and lost during capture. It will probably be necessary either to take both sexes of these species and fertilize the eggs artificially, or to hold males and females in artificial impoundments where natural impregnation can occur.

On the vessel, the shrimp are held in a tank through which water is circulated continuously. For the short trip from the dock to the laboratory, they are kept in 20-gallon plastic barrels. At the laboratory, the shrimp are usually placed singly in 100-liter, fiberglass tanks containing well-aerated water that has been passed through a 5μ cellulose filter.

During spawning, the shrimp releases many metabolites as byproducts which soon pollute the sea water, killing both eggs and larvae. Initially, antibiotics were used to attempt to control this contamination. The addition of sodium penicillin G and dihydrostreptomycin sulfate in concentrations of 50 iu and $50\mu g$, respectively, per ml of sea water prior to spawning, controlled contamination for 24 to 48 hours. During this time the eggs hatched, and larvae could be isolated.

We have now, however, developed a method of filtration which has made the use of antibiotics unnecessary (Fig. 1). One end of each 100-liter fiberglass tank, in which the ripe shrimp are placed, is fitted with a fine-mesh (0.12-mm opening) nylon screen. Water is drawn by pump from behind the screen and recirculated through a crushed-oyster-shell filter without loss of or damage to the eggs or larvae. The area of the screen must be large enough that the flow of water through it is almost imperceptible. If the screen is too small, larvae are drawn against it and trapped by the water flow. We have found it best to set up the apparatus and recirculate the water, to condition the filter, for several days before actual use.

Once the eggs have been spawned, the adult is removed from the tank to keep her from eating the eggs.

Shrimp larvae are rather hardy and are not injured by gentle handling. After hatching, the nauplii can be siphoned out of the large tank and caught on a stainless steel screen. Although the larvae suffer no perceptible damage in the process, care must be taken to keep the screen immersed at all times. The larvae can then be easily dispensed, for experimental studies, into any suitable container. We usually use 250-ml beakers containing about 100 ml of medium, which is changed daily.

Water in the large tanks is recirculated continuously until the first protozoeal stage is reached and feeding starts. Thereafter, the water, although aerated vigorously, is recirculated only intermittently, to minimize loss of food but still maintain cleanliness.

Shrimp larvae are positively phototropic. If reared under an overhead light source, they swim to the surface, become trapped by the surface tension, and die because they are too weak to break loose. Conversely, a light placed beneath the semitransparent fiberglass tanks causes larvae to congregate on the bottom. If the water above the light is aerated vigorously, the larvae are dispersed throughout the tank. The larvae can also be reared in the dark; light is not essential to their development.

MEDIA

The choice of a suitable medium in which to rear the larvae has been difficult because results have varied with the same type of medium in different rearing experiments. Even though spawning and hatching have been accomplished in water obtained both from the bay and from offshore, we have been unable until recently to rear larvae in unenriched sea water. Larvae were reared to postlarvae by using "B_5" medium (Wilson and Collier, 1955) and "Miquel's" medium (Lutz et al., 1937) with soil extract, but results were inconsistent. In the past several months, however, we have successfully reared larvae by adding only the sodium salt of the metal chelator EDTA to filtered sea water. With EDTA as an additive in a concentration of 1 gram per 100 liters of sea water, small mass cultures were reared successfully for the first time.

Ewald (1965) reported differences between the survival of pink shrimp larvae cultured in bay and oceanic waters. The survival of the later larval stages was considerably greater in the oceanic water. Our comparable experiments have produced inconclusive results. In one experiment, beakers holding larvae were divided into four equal lots, each containing different media: untreated offshore water, offshore water with EDTA, untreated bay water, and bay water plus EDTA. Postlarvae were subsequently obtained in the beakers containing offshore water plus EDTA, but all larvae in the other media died. The larvae used in the experiment were taken from a large tank containing bay water with EDTA. Even though larvae in the beakers containing the same medium died, those in the large tank developed to postlarvae.

The results of an early experiment designed to test the influence of sterilization of media and the addition of antibiotics on survival of larvae in both bay water and offshore water are shown in Table 1. Although all larvae died, a clear-cut difference was evident between both the two types of water and the treated and untreated water. Offshore water appeared to be a better medium than bay water, and autoclaved water and autoclaved water plus antibiotics were better than either offshore or bay water.

TEMPERATURE

Temperature greatly affects the rate of larval development. The results of an experiment to determine the effects of temperature on the development of brown shrimp are shown in Figure 2. Salinity during the experiment was 30o/oo. No larvae have undergone complete development below 24° C. Those reared at 18° C and 21° C were active during the nauplial substages but did not survive the molt to protozoea I. Those held at 24° C took considerably longer to develop than those held at either 27° C or 30° C. The first postlarva was obtained after 11 days at 30° C, 12 days at 27° C, and 15 days at 24° C. Temperatures above 30° C were not tried.

SALINITY

Two experiments were conducted to determine the effects of salinity on the development of brown shrimp larvae, but the larvae died during the first protozoeal substage. Brown shrimp larvae have been reared to postlarvae four times, however, and the salinity variation between experiments was fairly large. Larvae were grown in a mass culture with an initial salinity of 24.1o/oo that, with daily water changes, decreased to 20.5o/oo before the first postlarval stage was reached. The highest salinity at which they have been reared was 36.0o/oo. Thus, it would seem that even though brown shrimp larvae normally live in the more saline offshore water, high salinities may not be essential.

FOOD

Particulate food is not required during the nauplial stage. A diatom, *Skeletonema* sp., is used as food for the protozoeal substages and brine shrimp, *Artemia* sp., for the later stages. Larval mortality has been greatest at the molt to, and during, the first protozoeal substage. For example, brown shrimp on a diet of *Skeletonema* suffered about 25% daily mortality during the first protozoeal substage (Fig. 3). After the second protozoeal substage was attained, brine shrimp were added to the diet and mortality was greatly reduced. We think the heavy mortality during the first protozoeal stage is caused by a food deficiency and could probably be reduced greatly if the shrimp were fed a more nutritious food than *Skeletonema.*

Four other organisms tested as foods have given larval survival as good as or better than those obtained with *Skeletonema.* They were a diatom, *Thalassiosira* sp.; a monad, *Dunaliella* sp.; and two dinoflagellates, *Gymnodinium splendens* and *Exuviella* sp. Also, mixtures of food organisms gave better results than their individual components. In one experiment, all first protozoeae which were fed an unidentified diatom died after one day, but when this diatom was combined with *Exuviella* and *Thalassiosira,* survival of larvae was greater than that obtained with a mixture of only *Exuviella* and *Thalassiosira.*

Mass cultures of *Skeletonema* have been maintained as long as seven days by using the metal chelator EDTA as an additive in a concentration of one gram per 100 liters of sea water as recommended by Johnston (1964). Because the culture tanks are uncovered, they usually become contaminated after seven or eight days, even though the water is filtered through a Gelman metrical filter (0.80_{μ} pore size) and a type E glass-fiber prefilter before it is used. To assure a constant supply of diatoms for feeding, two 40-liter cultures are alternated; the second is started after the first is about four days old. Inoculated with one liter of diatom culture, the mass cultures usually reach a cell density of 92,000 per ml in about two days. This cell density is maintained by replenishing one-half the culture volume daily. Constant illumination of 1,000 foot-candles is supplied with fluorescent lights.

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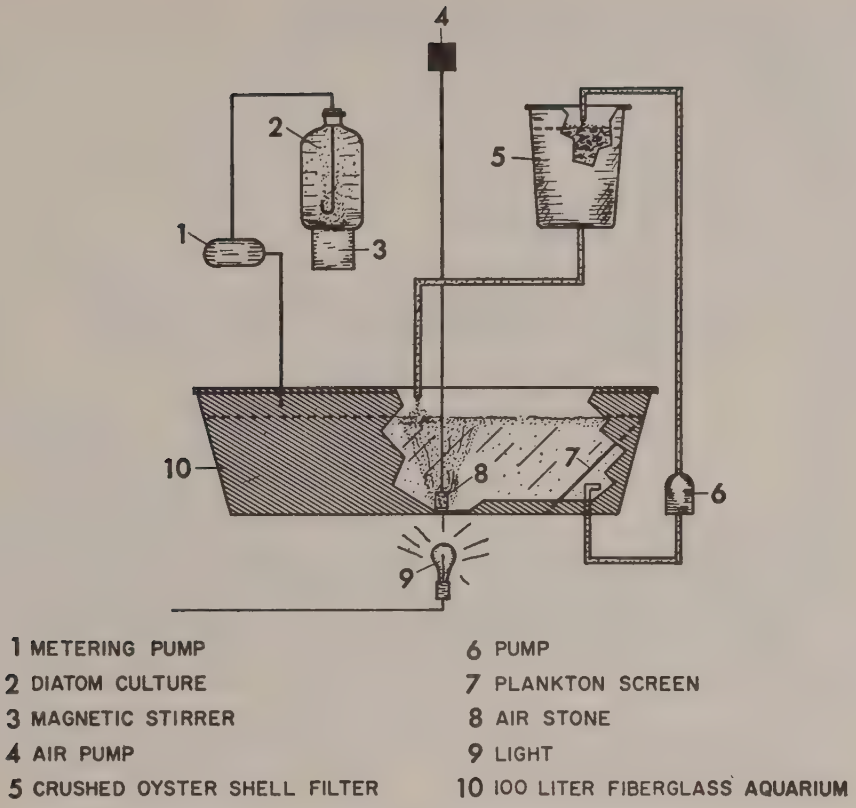
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2
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7
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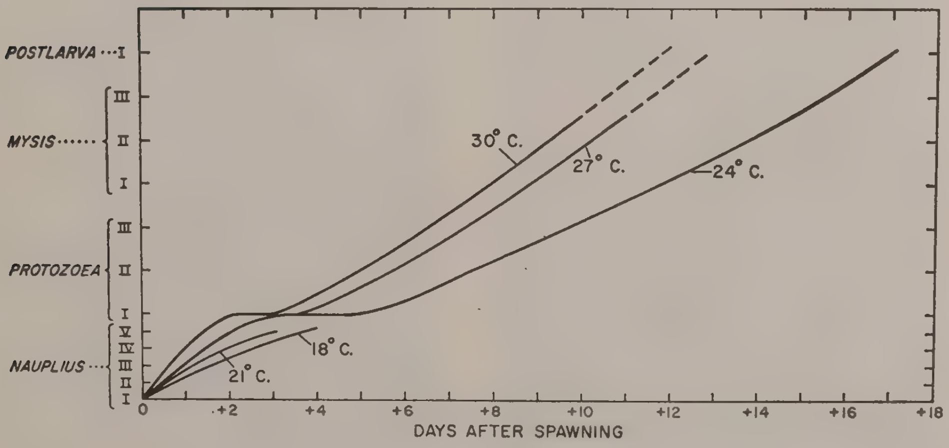
6
9
1 METERING PUMP
2 DIATOM CULTURE
3 MAGNETIC STIRRER
4 AIR PUMP
5 CRUSHED OYSTER SHELL FILTER
6 PUMP
7 PLANKTON SCREEN
8 AIR STONE
9 LIGHT
10 100 LITER FIBERGLASS AQUARIUM

Figure 1. Apparatus used to rear larval shrimp.



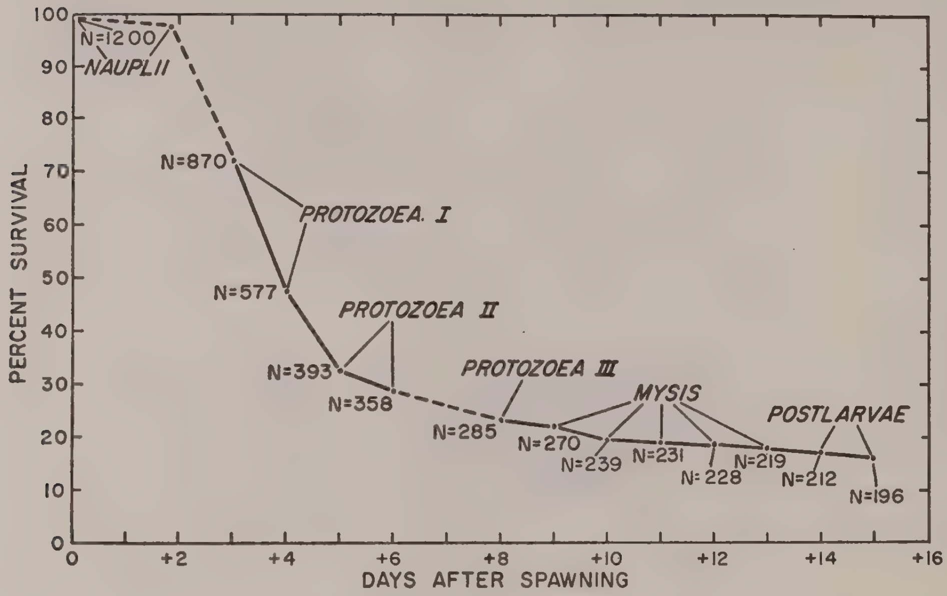


Figure 3. Survival of brown shrimp larvae, N = number of larvae.

Table 1. Number and stage of development of larval brown shrimp surviving after culture in different media (N = nauplii, P = protozoeae).

	Days after hatching					
Type of water and treatment	0	1	2	3	4	5
Untreated bay	25N	22N	0	0	0	0
Bay + antibiotics	25N	24N	7N	0	0	0
Autoclaved bay	25N	23N	19N	0	0	0
Autoclaved bay + antibiotics	25N	24N	23N	13N 10P	0	0
Untreated offshore	25N	22N	22N	9N 9P	0	0
Offshore + antibiotics	25N	24N	24N	8N 16P	0	0
Autoclaved offshore	25N	24N	24N	23P	20P	0
Autoclaved offshore + antibiotics	25N	25N	25N	25P	13P	0

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Migration and Population Estimation of the Tautog, *Tautoga onitis* (Linnaeus), from Rhode Island

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ABSTRACT

Approximately 3,000 adult tautog (*Tautoga onitis* Linnaeus), were tagged with fluorescent ribbons at four spawning locations in the West Passage of Narragansett Bay during the spring of 1961. The distribution of 230 tag returns over a 2½-year period indicated that the Narragansett Bay tautog is local to Rhode Island's coastal waters. The adult population inhabits the bay and inshore waters from early May until late October. During the winter, tautog occupy deeper areas with rugged bottom topography, where they are relatively dormant and forage little for food.

Discrete spawning groups exist in the northern half of the bay during May and June. These groups are thoroughly mixed during the remainder of the year. A high percentage of adults returned to the same spawning locations in the upper portion of Narragansett Bay in the spring of 1962.

The size of the Rhode Island population of adult tautog was estimated by the Schnabel and Schumacher multiple-census methods. Twenty-two census samples were obtained by divers counting the number of tagged and nontagged fish underwater. Estimates ranged from 300,000 to 400,000.

INTRODUCTION

The tautog, *Tautoga onitis* (Linnaeus), is a popular marine sport fish of Rhode Island. Knowledge of the life history of this species is of fundamental importance to the management of the fishery. Identification of stocks, determination of seasonal migration, and population estimation were the objectives of this study.

The species is restricted to the coastal regions of eastern North America from Nova Scotia to South Carolina; it is most abundant between Cape Cod and the Delaware Capes (Bigelow and Schroeder, 1953). Tautog are seldom observed before late April or after November in any part of their geographical range. The species is thought to spend the winter in the deeper inshore waters in a relatively inactive state. North of Cape Cod it is unusual to catch one more than 3 or 4 miles from land or at depths greater than 30 to 60 feet. South of the Cape they range farther and deeper, and are one of the more common fishes caught in 60 to 80 feet on the Cholera Bank, 10 to 12 miles offshore from Long Island (Bigelow and Schroeder, 1953). At the other extreme, they commonly feed in the intertidal zone during high tide. They occasionally enter brackish water but are not known to enter freshwater.

Cooper[1] demonstrated that the Rhode Island tautog reaches an age of at least 34 years. Males grow faster than females, attaining an L_∞ of 665 mm compared with 506 mm for females. Both sexes are mature when 3 years old (200 mm for males and 190 mm for females). Tautog enter the sport and commercial fisheries at about 275 mm. The species is

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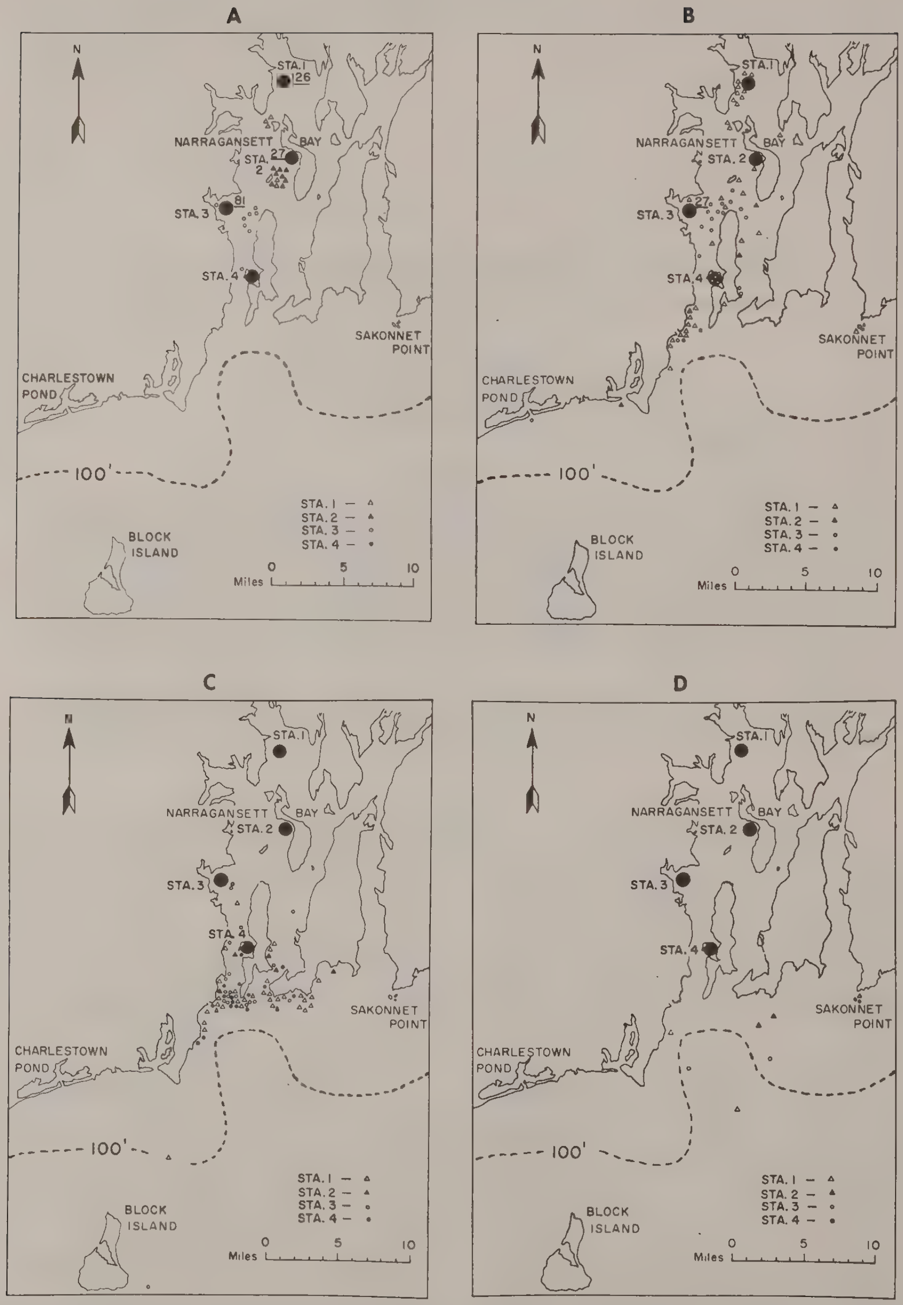
[1] Cooper, Richard A. 1965. Life history of the Tautog, *Tautoga onitis* (Linnaeus). Ph.D. thesis. Graduate School of Oceanography, Univ. of Rhode Island, Kingston, 153 p.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B
C
D
N
STA. 1
126
27
NARRAGANSETT
BAY
STA. 2
81
STA. 3
STA. 4
SAKONNET POINT
CHARLESTOWN POND
100'
BLOCK ISLAND
STA. 1 — △
STA. 2 — ▲
STA. 3 — ○
STA. 4 — ●
0 5 10
Miles

FIGURE 1.—Distribution of returns of tagged fish released at four stations in Narragansett Bay. A. 15 May to 15 June 1961. B. 16 June to 15 July 1961. C. 16 July to 31 October 1961 and 1962. D. November 1961 and 1962. Symbols indicate station at which recovered fish had been released. Underlined numbers in A and B represent fish recaptured at the same station at which they were released.

primarily a sport fish, taken by rod-and-reel fishermen and spearfishermen from May through October within Narragansett Bay and the adjacent coastal waters. It is the most abundant fish in the catch of spearfishermen. From May through July, commercial fishermen catch approximately 4,000 adult tautog while dragging for flounders in the bay. Relatively few tautog are taken by draggers outside the bay at any time of the year.

METHODS

Knowledge of the spring spawning aggregations of tautog in Narragansett Bay led to the selection of four tagging stations in the west passage of the bay (Figure 1). Fish samples were obtained with otter trawls. During May, June, and July 1961, 2,970 adult tautog (≧ 275 mm total length) were tagged and released at the four stations (Table 1).

The tag was a strip of fluorescent vinyl plastic, 356 mm long, 12.7 mm wide, and 0.36 mm thick. One end of the tag was pushed through the dorsal musculature of the fish just beneath the posterior soft-rayed portion of the dorsal fin, with the aid of a "sailmakers needle." The ends were tied in a figure-eight knot, leaving clearance for the dorsal fin in an erected position. A pattern of punched holes and clipped corners in the tag permitted identification of individual fish. Yellow tags were used at stations 1 and 2, orange at station 3, and green at station 4.

Newspaper, television, and radio coverage of the study was provided in Massachusetts, Rhode Island, Connecticut, and New York. Notices were sent to skin-diving clubs in these states. Members of several Rhode Island skin-diving clubs made dives throughout the year along Rhode Island's coastline in search of tagged tautog. In addition, from 15 May to 15 June 1962, 145 hours were spent trawling the inshore areas of West Passage from station 1 to station 4. The Rhode Island Division of Fish and Game paid a $1.00 reward for the return of each tag.

An estimate of the rate of tag shedding was obtained by observing 30 tagged and 30 untagged individuals held in an indoor aquarium 30 feet by 4 feet by 2 feet. The experiment began on 3 May 1961, and was terminated after 85 days due to supersaturation of gases in the water. A daily record was kept of tag loss, mortality, and the condition of the fish. Mortality due to tagging was negligible.

TABLE 1.—*Station and number of tautog tagged in Narragansett Bay in 1961*

Station 1		Station 2		Station 3		Station 4	
Date	Number tagged	Date	Number tagged	Date	Number tagged	Date	Number tagged
13 May	37	24 May	95	22 May	146	21 June	10
20 May	332	28 May	38	25 May	182	27 June	66
21 May	315	1 June	99	1 June	83	28 June	16
27 May	378	2 June	64	2 June	89	8 July	128
10 June	212	3 June	38	5 June	176	9 July	76
14 June	147	—	—	8 June	115	—	—
—	—	—	—	13 June	24	—	—
—	—	—	—	19 June	79	—	—
—	—	—	—	21 June	25	—	—
Total	1,421		334		919		296

Modified Schnabel and Schumacher population estimates (Ricker, 1958) were made of the adult tautog population inhabiting the area of dispersal during the summer and fall of 1961. Estimates were based on 22 census samples taken by swimming for 2 hours, with SCUBA equipment, along the coastline or along an offshore reef and counting the number of tagged and untagged fish (Figure 2).

RESULTS

Migration

A total of 230 tags were returned between May 1961 and October 1963. Figure 1A illustrates the distribution of tag returns for 15 May to 15 June 1961. Most of the fish recaptured at stations 1, 2, and 3 had been tagged at those respective locations; spawning groups apparently were discrete. No fish were available for tagging at station 4 before 21 June.

The distribution of tag returns from 16 June to 15 July 1961 indicated the continued presence of a relatively discrete spawning group at station 3 (Figure 1B). Of 306 fish caught at station 4, 10 were recaptured fish, of which 3 came from station 1, 1 from station 3, and 6 from station 4; this record suggests a mixture of fish from the more northern spawning areas. By 15 July, the spawned portion of the population had spread eastward to Sakonnet Point and westward to Charlestown Pond.

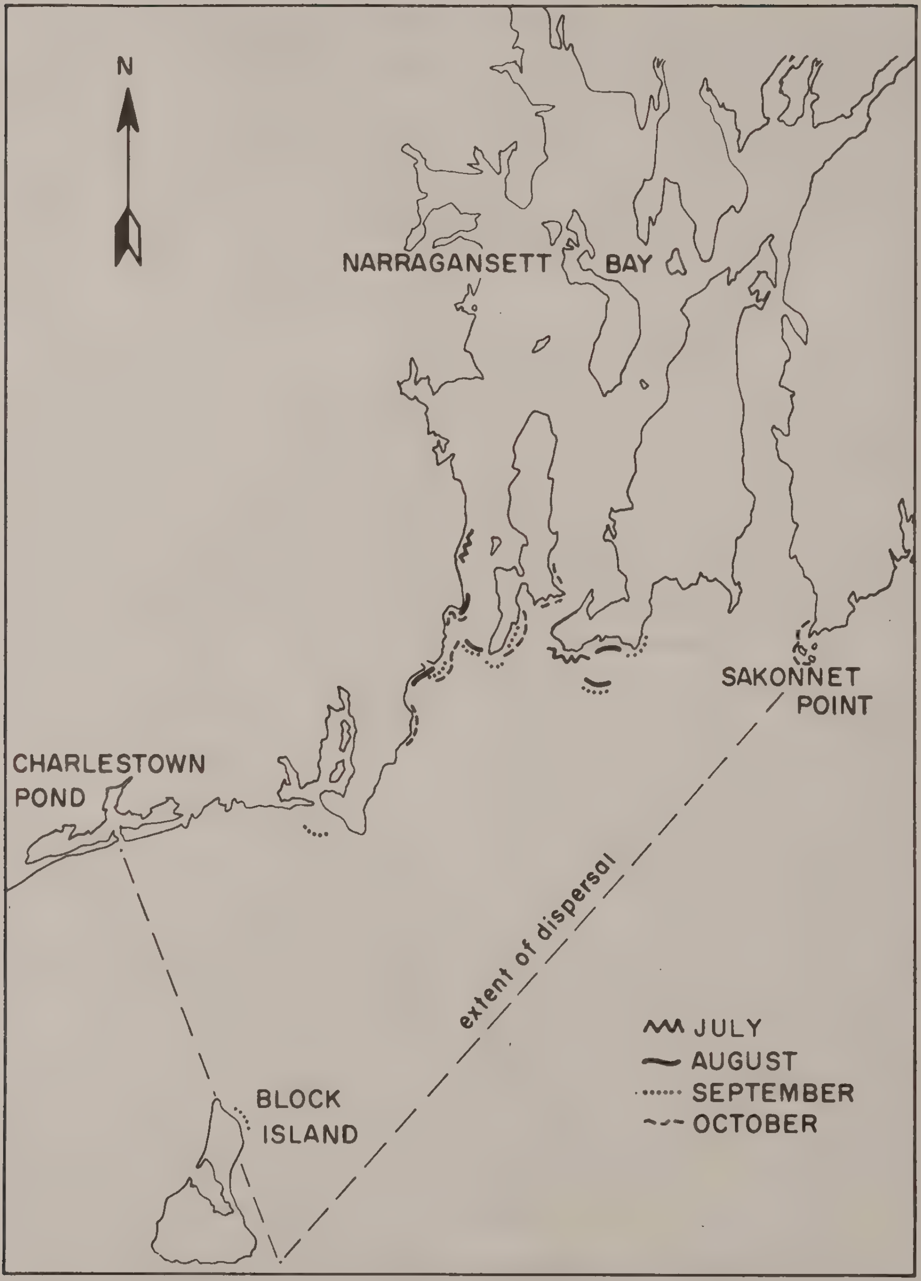

N
NARRAGANSETT BAY
SAKONNET POINT
CHARLESTOWN POND
extent of dispersal
BLOCK ISLAND
JULY
AUGUST
SEPTEMBER
OCTOBER

FIGURE 2.—Locations of 1961 census samples made by divers.

TABLE 2.—*Census data and correction data in tagging study of tautog in Narragansett Bay*

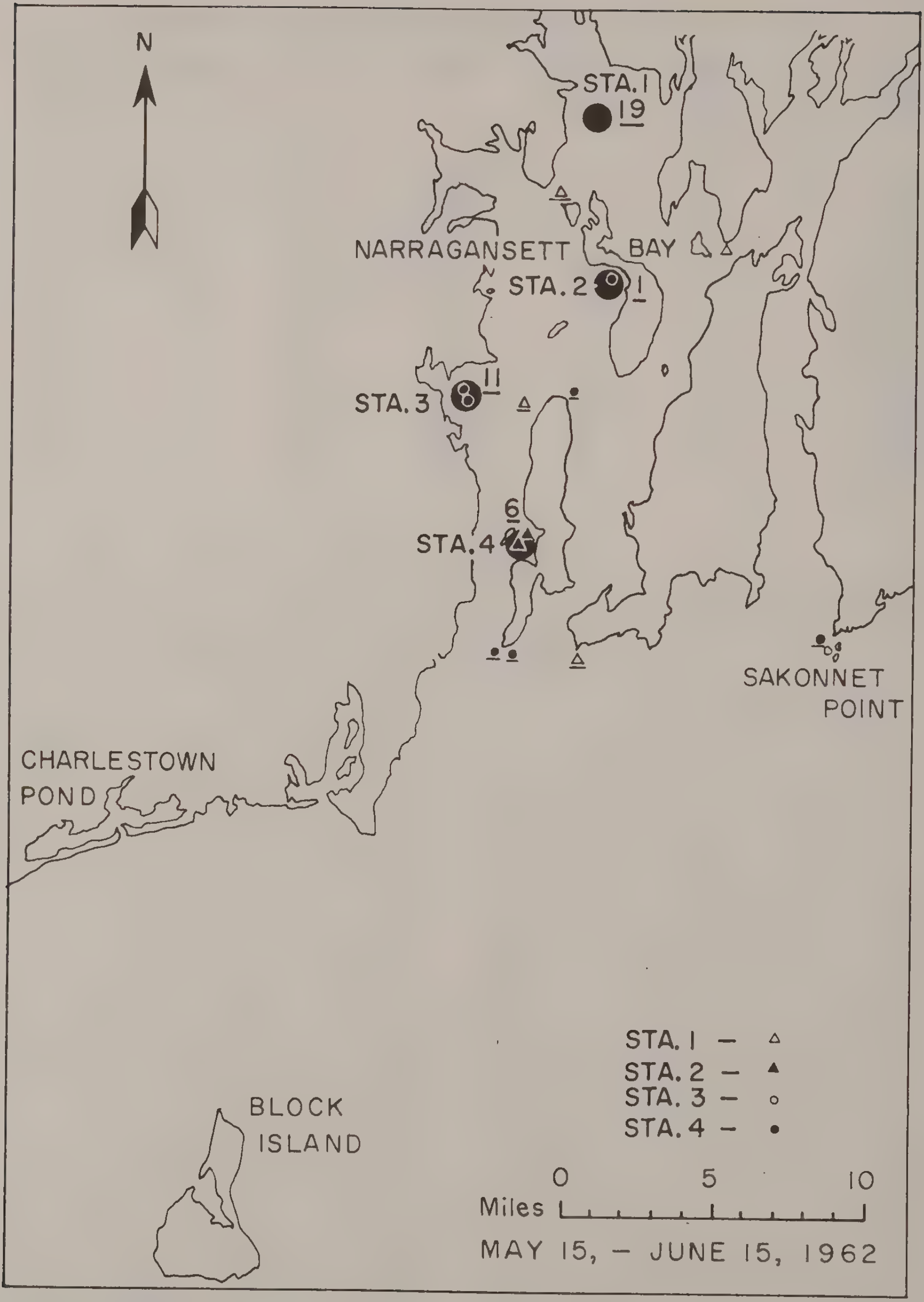
Date of census sample (1961)	Cumulative tag returns to date of census sample R_t	Time from mean tagging date (days)	Percentage of tags lost	Total sample size C	Number of tagged fish seen R	Number of tagged fish in population at start of census sample (corrected) M
27 July	57	61	24.8	201	0	1,485
28 July	57	62	25.8	305	0	1,465
3 August	58	68	28.8	347	0	1,401
5 August	59	70	29.7	450	1	1,383
6 August	59	71	30.2	517	2	1,373
9 August	59	74	31.7	5	1	1,342
30 August	68	95	42.0	637	5	1,121
1 September	68	97	43.0	80	0	1,101
4 September	76	100	44.5	153	1	1,062
5 September	78	101	45.0	98	1	1,050
6 September	78	102	45.5	130	0	1,039
8 September	78	104	46.5	40	0	1,019
9 September	79	105	47.0	224	0	1,008
11 September	79	107	47.9	41	0	990
12 September	79	108	48.4	131	1	979
9 October	82	135	61.7	148	0	703
10 October	82	136	62.2	600	1	693
12 October	84	138	63.2	309	0	670
14 October	86	140	64.2	536	1	648
16 October	86	142	65.2	253	0	628
18 October	86	144	66.1	397	1	609
27 October	87	153	70.6	100	0	516

The spring migration to the spawning grounds is presumed to involve movement north along the channels of the bay. If the search for a specific spawning location during May and early June, when catch-per-unit effort increased at stations 1, 2, and 3, were exclusively a random search, many of the fish tagged at one station should have been recaptured at other stations. Since discrete spawning groups were demonstrated at these stations, random search alone seems unlikely.

Figure 1C shows the distribution of tag returns for the periods 16 July to 31 October 1961 and 1962. Tag-return data for 1961 and 1962 have been combined to give a more representative picture of tautog distribution. During this time interval the adult population primarily inhabited the rocky inshore region near the mouth of the bay. Some fish, however, had moved offshore as far as the southern end of Block Island. Fish of the different spawning groups were mixed at the mouth of the bay. Observations by divers and the distribution of tag returns indicated that relatively few adult tautog were in the northern half of the bay at this time.

The distribution of tag returns for November 1961 and 1962 suggested a general movement offshore into water 80 to 150 feet deep (Figure 1D), in the vicinity of rugged bottom topography. This movement explains why commercial fishermen, who fish otter trawls only in areas with relatively smooth bottom, catch very few tautog during the winter. During the winters of 1961–62 and 1962–63, divers could find no adult tautog in the inshore regions to depths of 50 feet. In December 1961 several adult tautog were seen at 80–90 feet, about 2 miles offshore. The fish were dormant, lying on their sides or in upright positions in crevices at the bottom. Bottom water temperature was 7.5 C. The stomachs and intestinal tracts of three tautog that were captured were greatly reduced in size and devoid of food. Twelve additional adults were obtained from commercial fishermen during December; only two had food in their stomachs (remains of rock crabs, *Cancer irroratus*). It thus appears that adult tautog are relatively inactive during the winter. No tags were returned from the end of November 1961 and 1962 until early May of the following years.

From 15 May to 15 June 1962, most of the recaptured fish were caught at the tagging stations. All of the 19 tagged fish taken at station 1, 1 of 2 at station 2, 11 of 13 at station 3, and 6 of 8 at station 4 had been tagged at the point of capture (Figure 3). Tautog tend therefore to return to the same spawning area each year. The seven fish recaptured by rod-and-reel fishermen in areas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STA. 3 — ○
STA. 4 — ●
0 5 10
Miles
MAY 15, — JUNE 15, 1962

FIGURE 3.—Distribution of tag returns from 15 May to 15 June 1962. Underlined numbers represent recoveries (by trawling) at the station of release; underlined symbols are returns from sport fishermen in nonspawning areas.

Table 3.—*Modified Schnabel and Schumacher population estimates, with 95% confidence limits, of Rhode Island adult tautog population*

Date (1961)	Modified Schnabel	95% Confidence limits	Schumacher	95% Confidence limits
5 August	926,903	325,694—12,513,665	1,908,640	524,426— *
6 August	640,912	290,005— 2,563,648	875,335	355,059— *
9 August	514,071	249,484— 1,671,985	662,267	99,154— *
30 August	328,443	191,869— 695,569	399,399	104,374— *
1 September	337,251	197,015— 714,223	408,154	114,918— *
4 September	321,363	191,905— 652,284	386,660	121,463— *
5 September	303,158	184,574— 593,423	364,067	125,666— *
6 September	314,414	191,427— 615,456	374,709	133,555— *
8 September	317,811	193,495— 622,105	377,858	139,603— *
9 September	336,627	204,951— 658,936	395,116	148,474— *
11 September	340,009	207,011— 665,558	398,163	153,831— *
9 October	331,723	205,481— 629,262	384,674	160,656— *
10 October	337,729	212,468— 623,251	386,125	166,823— *
12 October	352,516	221,772— 650,541	395,460	172,915— *
14 October	352,170	224,684— 634,240	393,449	177,588— *
16 October	362,763	231,442— 653,317	399,883	182,709— *
18 October	354,516	229,089— 624,698	393,494	184,876— *
27 October	357,741	231,173— 630,381	395,146	188,287— *

of rugged topography may have been en route to or from one of the spawning areas. Chenoweth[2] found no evidence that spawning occurred in these rough bottom environments. Totals of 29, 8, and 3 fish caught at stations 1, 3, and 4, respectively, had scars in the dorsal musculature which indicated that tags had been lost. This absence of scarred fish in the trawl catches at other spawning areas further suggests a high degree of homing.

Population Estimation

The validity of the population estimates (N) depends on the fulfillment of five assumptions (Cooper and Lagler, 1956): (1) tagged fish retain their tags throughout the period of population estimation and are recognized upon recapture; (2) tagged fish are randomly redistributed throughout the population, and netting effort is proportional to population density; (3) tagged and untagged fish are equally susceptible to capture; (4) the population is a closed system without recruitment by growth or immigration; and, (5) loss by mortality or emigration is proportionately the same for tagged and untagged fish.

The sighting of tautog with orange tags was omitted because it was apparent by early June 1961 that the orange tags were rapidly tearing their way through the dorsal musculature of the fish and would soon be lost. These plastic strips were relatively thick (0.45 mm as compared to 0.36 mm for the yellow and green material) and were therefore less pliable and more likely to tear out.

The linear relationship between accumulative percentage of tags lost (L) as a function of time in days (T) obtained from the holding experiments is expressed by the equation, $L = 0.492T - 4.681$; the correlation coefficient was 0.970. This equation was used to adjust the value of M (number of tagged fish in the population). The date of 28 May 1961, was chosen as the mean tagging date and designated as time zero in the above relationship. Adjustments in M as a function of time were calculated, and the number of yellow and green tag returns (R_i) were subtracted to obtain the corrected M. Table 2 lists the values of C (sample size), R (recaptures in sample C), corrected M, and the associated correction factors.

Table 3 lists the modified Schnabel and Schumacher (maximum likelihood) estimates of N with their 95% confidence limits. The first three estimates are omitted because no tagged fish had been seen. A positive upper confidence limit for the Schumacher estimate could not be calculated by the formulae of Ricker (1958) and DeLury (1958). A negative argument was incurred.

Observations by divers indicated that the distribution of untagged individuals was similar to the distribution of tag returns in August, September, and October, 1961 and 1962. Also, numbers of fish seen was proportional to population density.

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[2] Chenoweth, Stanley B. 1963. Spawning and fecundity of the tautog, *Tautoga onitis* (Linnaeus). M.S. thesis. Graduate School of Oceanography, Univ. of Rhode Island, Kingston, 60 p.

Tagged fish may be more readily seen underwater than untagged fish near the limit of visibility, but all except one of the sightings were made well within this limit. The underestimation of N resulting from overestimating the ratio of tagged to untagged fish seen is assumed to be unimportant.

The population is not a closed system in terms of recruitment by growth. Tautog which were 264 mm long on 28 May had grown to 275 mm by 1 September. The earliest acceptable estimates of N were chosen as the most reliable. The trend in population estimates with time suggests, nevertheless, that immigration by untagged tautog did not occur during the study (Table 3). Also, the distribution of tag returns (Figures 1B and 1C) indicated that emigration did not occur. In terms of movements of individuals, the population was considered closed.

Loss of tagged fish from the population by mortality is considered negligible. Interviews with spearfishermen indicated that most, if not all, of the tags recovered had been reported. Such was not true for the rod-and-reel fishermen or the commercial fishermen. If fishermen were not selective for or against tagged individuals, error would not be introduced in the estimation of N.

DISCUSSION

Selective predation on small yellow perch, *Perca flavescens*, tagged with opaque yellow tags, has been demonstrated (Lawler and Smith, 1963). Tagged tautog, however, ranged from 275 mm to 640 mm long. The only piscivorous fish in the study area large enough to capture and devour tautog in this size range are the striped bass, *Roccus saxatilis*, and several species of sharks. The tautog is not included in the list of major food organisms taken from the stomachs of striped bass from the waters around Cape Cod (Bigelow and Schroeder, 1953) or from Chesapeake Bay (Hildebrand and Schroeder, 1928). No information is available concerning predation by sharks.

A source of error in the method of census sampling resulted in underestimation of N. It was demonstrated that fish length was overestimated during the underwater count of untagged fish by approximately 30 mm; this error causes an underestimate of N.

Cooper and Lagler (1956) defined a "good" estimate as "one which approaches population size within limits of approximately ± 5% and one which must reach a stage of leveling off, in a day to day sequence, forecasting relatively little subsequent change if extended in the future." It is unrealistic to assume, with only 0.29% of the population marked as of 30 August and 0.14% as of 27 October, that these estimates are within 5% of the true population size. The criterion of leveling off, however, established from 30 August to 27 October, suggests a good estimate.

A partial check on the relative accuracy of these population estimates was obtained by comparing the number of commercially-caught tagged and untagged fish, taken within the prescribed limits of migration (Figure 2) during June through October. Monthly landings of tautog at Point Judith and Newport, Rhode Island, were obtained from the Bureau of Commercial Fisheries, U. S. Fish and Wildlife Service, Woods Hole, Massachusetts, and were compared with the number of tags in this catch. The 7,261 pounds represents a catch of approximately 4,149 fish (assuming an average weight of 1.75 pounds). Accepting 31 August as the mean date during the above 4-month period gives a time interval of 95 days during which tags were being shed. The corrected M is therefore 929. By the single-census method of Petersen where,

$$N = \frac{M\,(C+1)}{(R+1)}$$

and putting $M = 929$, $C = 4{,}149$, and $R = 9$, N is computed as 385,535. At assumed average fish weights of 1.50 pounds ($C = 4{,}841$) and 2.00 pounds ($C = 3{,}631$), the computed values of N are 449,822 and 337,320, respectively. These estimates are in fair agreement with those made from census samples collected by divers.

The adult tautog population which spawns in Narragansett Bay is fished by sport and commercial fishermen throughout the spring, summer and fall along much of Rhode Island's coastline. Movement into and out of this coastal area by adults is negligible. Although discrete spawning groups were demonstrated in upper Narragansett Bay, a high degree of mixing was evident when the species was dispersed after spawning. The Rhode Island tautog population can therefore be considered a unit stock. This stock is not necessarily a genetic or biological unit. The term is used to indicate that, for practical purposes, regulations and estimates of parameters can apply to the Rhode Island population as an entity, independent of adjacent coastal populations.

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BRACHYCOELIUM AMBYSTOMAE SP. N. (TREMATODA: BRACHYCOELIIDAE) FROM *AMBYSTOMA OPACUM*

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BRACHYCOELIUM AMBYSTOMAE SP. N. (TREMATODA: BRACHYCOELIIDAE) FROM *AMBYSTOMA OPACUM*

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ABSTRACT: *Brachycoelium ambystomae* sp. n. is described from the marbled salamander, *Ambystoma opacum* (Gravenhorst), from Leon County, Florida. This species differs chiefly from the 11 other described members of the genus by its spination, distribution and development of vitellaria, position and size of its ovary and testes, and body length. Specimens of the genus *Desmognathus* from the same locality were not infected with this trematode.

Nine marbled salamanders, *Ambystoma opacum* (Gravenhorst), collected in Leon County, Florida, in November 1961, harbored trematodes of the genus *Brachycoelium.*

Byrd (1937) reported the possibility that 13 well defined species were included in this genus. Rankin (1938) reduced all 14 described species to synonymy with the type species, *Brachycoelium salamandrae* (Frölich, 1789). Parker (1941) and Cheng (1958), after careful studies, agreed that specimens which they collected possessed diagnostic characters of some particular species and not of others. Cheng (1958) and Cheng and Chase (1961) reported that there were enough distinct characters, e.g., shape and position of testes and distribution of vitellaria, to recognize 11 species in the genus *Brachycoelium.*

Careful study of the specimens from northwest Florida indicated that on the basis of their extensive spination, development and distribution of vitellaria, size of testes and ovary, and body length, they represent a new species, here designated as *Brachycoelium ambystomae.*

METHODS

Specimens were removed from the small intestine of the hosts, fixed for whole mounts with alcohol–formol–acetic solution at room temperature, under slight cover-slip pressure, and stained with Semichon's acetocarmine. Two flattened and two unflattened worms, fixed in hot AFA and stained with acetocarmine, were sectioned frontally for internal study. The figures presented are composite drawings made from whole mounts and sectioned worms with the aid of a microprojector and camera lucida. This description is based on the study and measurements of 20 worms. All measurements are in microns unless otherwise indicated. Average measurements are given with ranges in parentheses.

Brachycoelium ambystomae sp. n.

(Figs. 1–4)

Description

Body slightly ovoid (under cover-slip pressure) and elongate (Figs. 1, 2); 1.49 mm (1.01 to 2.36) long; 0.48 mm (0.34 to 0.70) wide at level of testes; fine cuticular spines (Fig. 1) covering entire body. Oral sucker subterminal, 215 (187 to 297) in diameter; acetabulum, 133 (111 to 187) by 105 (100 to 110), 440 (410 to 700) from anterior end; prepharynx short; pharynx oval, 64 (52 to 78) wide; esophagus 123 (77 to 275) long; ceca short, divergent, terminating anterior to acetabulum. Vitellaria compact, dorsal, extending from level of prepharynx to level of ovary; filling lateral fields in all specimens, approaching median field in a few, but not occupying middle of body in any (Figs. 1, 2). Ovary subspherical, 104 (77 to 187) by 95 (74 to 102), either on left or right of body at level of acetabulum; oviduct arising from lateromedial margin of ovary, extending to ootype (Fig. 4). Ootype usually immediately dorsal to acetabulum. Laurer's canal extending from dorsal surface of ootype to minute opening on dorsal surface slightly posterior and to the right of level of ootype (Fig. 4). Seminal receptacle large, between ovary and ootype, joining ootype near junction of Laurer's canal. Mehlis' gland indistinct. Vitelline duct incompletely traced from ootype; uterus extending posteriad from ootype (Fig. 4), apparently following a transverse looping path to posterior end of body, then anteriad to the shallow genital atrium which lies slightly left of median immediately anterior to acetabulum. Eggs yellow-brown, oval, operculate, 44 by 31 (Fig. 3). Testes ovoid, 153 (110 to 220) by 145 (110 to 187), on same level, lateral, and slightly anterior to midbody but posterior to acetabulum. Vasa efferentia extending from anteromedial surface of testes to seminal vesicle. Vas deferens not observed. Cirrus pouch anterior to, and slightly overlapping, acetabulum dorsally; cirrus extending anteriorly from seminal vesicle, looping back ventroposteriad to genital atrium which opens externally through common genital pore on median ventral surface immediately anterior to acetabulum (Fig. 4). Excretory bladder I type; excretory pore posterior, terminal.

Type host: Ambystoma opacum (Gravenhorst).

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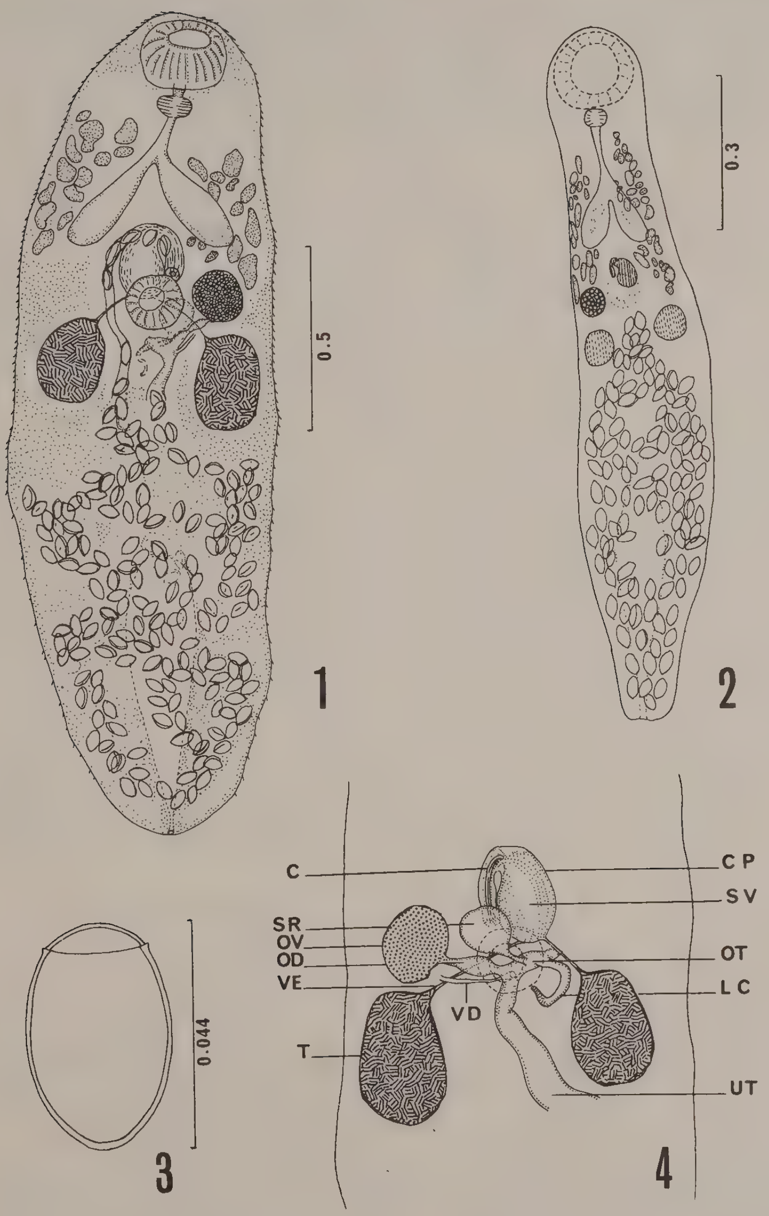

FIGURES 1–4. *Brachycoelium ambystomae* sp. n. from the marbled salamander in Florida. (Scales are in millimeters.) **1**. Ventral view of whole mount fixed with moderate pressure. **2**. Dorsal view of whole mount fixed without pressure. **3**. Uterine egg from whole mount. **4**. Dorsal view of reproductive systems from whole mount. Abbreviations: C, cirrus; SR, seminal receptacle; OV, ovary; OD, oviduct; T, testis; VE, vasa efferentia; VD, vitelline duct; SV, seminal vesicle; OT, ootype; LC, Laurer's canal; UT, uterus; CP, cirrus pouch.

Habitat: Small intestine.

Type locality: Ochlockonee River, Leon County, Florida.

Incidence: All of nine specimens of *Ambystoma opacum* infected.

Specimens deposited: Holotype, USNM Helm. Coll. No. 60690; one paratype, USNM Helm. Coll. No. 60691.

DISCUSSION

Brachycoelium ambystomae is the first new species of *Brachycoelium* to be described from Florida and the fourth from *Ambystoma opacum.* Only one other species, *B. hospitale* (Stafford, 1900) Looss, 1902, has been reported from Florida (Manter, 1938). This species has been placed in synonymy with *B. salamandrae* by Rankin (1938) and Cheng (1958). Others reported from *A. opacum* are *B. salamandrae* (Frölich, 1789); *B. storeriae* Harwood, 1932; and *B. louisianae* Byrd, 1937. Each of these species is distinct from *B. ambystomae* in body length. In addition, *B. salamandrae* has a wider body, less spination, and more rounded testes than *B. ambystomae*. The vitellaria of *B. storeriae* and *B. louisianae* fill the median fields of their forebodies, whereas the vitellaria of *B. ambystomae* are largely restricted to the lateral zones (Figs. 1, 2).

B. obesum Nicoll, 1914; *B. daviesi* and *B. meridionalis* Harwood, 1932; *B. louisianae* Byrd, 1937; *B. elongatum* Cheng, 1958; and *B. stablefordi* Cheng and Chase, 1961, are distinct from *B. ambystomae* in body shape, length of esophagus, position of testes, and distribution of vitellaria.

B. mesorchium Byrd, 1937 differs from *B. ambystomae* in that the former's spination extends only to the level of its testes, and its testes are on two distinct levels relative to one another, and are spindle-shaped. In addition the distribution of the vitellaria of *B. mesorchium* (USNM type specimen No. 9031) is more extensive than that of *B. ambystomae*.

This new species most closely resembles *B. trituri* Holl, 1928. Careful comparison of specimens of *B. ambystomae* with descriptions of *B. trituri* by Holl, 1928; Byrd, 1937; Cheng, 1958; and the USNM type specimen No. 7994 of *B. trituri* reveal the following differences. Spination is complete for *B. ambystomae*; spines extend only over anterior two-thirds of body on *B. trituri*. The ovary may occur on either the left or right side of the body in different specimens of *B. ambystomae*, whereas it is reported and figured as occurring only on the right side in *B. trituri* by Holl, Byrd, and Cheng, and it occurs on the right in the type specimen (No. 7994). The vitellaria of *B. ambystomae* extend from the level of the prepharynx to the level of the ovary and approach the median dorsal field, whereas the vitellaria of *B. trituri* are more restricted to the lateral zones of the body posterior to the pharynx and anterior to the terminal lobes of the ceca. The ovary (104 by 95) and testes (153 by 145) of *B. ambystomae* are consistently larger than the ovary (91 by 53) and testes (95 by 76) of *B. trituri*. Of lesser significance, perhaps, are the differences in hosts and reported localities of the two species.

Ten salamanders of the genus *Desmognathus*, from the same locality as the hosts of *B. ambystomae,* were free of trematodes. Brandon (1965) found 13 specimens of *Desmognathus monticola* from Butler County, Alabama, to be without flukes. However, 13 specimens of another salamander, *Phaeognathus hubrichti*, from the same locality harbored many adult *Brachycoelium salamandrae*. Brandon discovered that *D. monticola* apparently had not fed on snails (possible vectors of brachycoeliids), whereas seven infected *P. hubrichti* contained snail remnants. These observations suggest that the selective feeding habits of potential brachycoeliid definitive hosts may account for presence or absence of the worms.

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Short Papers and Notes

Two Peritrichous Ciliates from the Gills of the Blue Crab

ABSTRACT: Peritrichous ciliates of the genera *Lagenophrys* and *Epistylis* were found on the gill lamellae of 32 of 41 blue crabs from Chincoteague and Chesapeake Bays. The species of *Lagenophrys* reported here is the first from a marine brachyuran host and may represent a new species. The specific taxonomic position of the *Epistylis* species has not yet been determined. The occurrence of these ciliates in great numbers on gills of moribund blue crabs raises a question as to whether or not they may contribute to mortality of crabs in shedding or holding tanks.

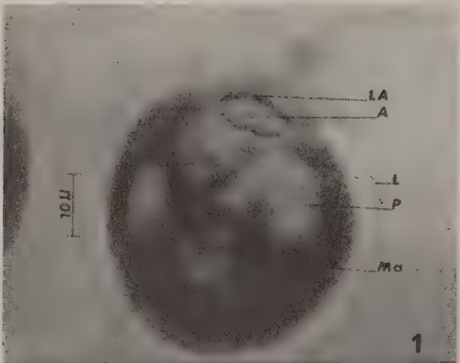
While examining gills of moribund blue crabs (*Callinectes sapidus*) from holding tanks at the substation of the U. S. Bureau of Commercial Fisheries, Greenbackville, Virginia, I found attached peritrichous ciliates of two genera. Epibionts of the loricate genus *Lagenophrys* Stein (Peritrichida: Lagenophryidae) were firmly cemented to the surfaces of gill lamellae, each occupying or covering an area equal to the size of its lorica (Figs. 1, 2). Members of the stalked genus *Epistylis* Ehrenberg (Peritrichida: Epistylidae) were attached individually or in groups to lamellae by a single basal disk, or holdfast. *Lagenophrys,* as individuals or in groups, occupied a much larger gill surface area than did the *Epistylis.* Subsequently, I examined 41 blue crabs from Chincoteague and Chesapeake Bays; of these 32 had one or both ciliates, and both genera of ciliates were found in salinities that ranged from 11‰ (Tred Avon River, Md.) to 30‰ (Chincoteague Bay, Va.) (Table 1).

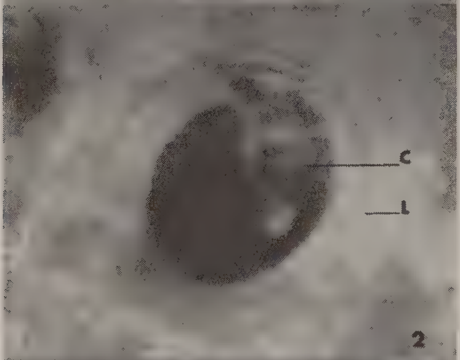
The genus *Lagenophrys* contains 51 described species (Corliss and Brough, 1965; Kane, 1965). The species in this genus have been reported from different distinct genera of crustacea. Most species have demonstrated a high degree of host-specificity. Corliss and Brough have stated, "Within reasonable limits, host-specificity is justifiably used as a taxonomic criterion for species of *Lagenophrys.*" Only one other species of *Lagenophrys* has been reported from a true crab: *L. metopauliadis* Corliss and Brough, 1965 from the fresh water brachyuran *Metopaulias depressus* of Jamaica. To my knowledge, the present report is the first of a species of *Lagenophrys* occurring on the branchiae of *Callinectes sapidus,* and the second report of a *Lagenophrys* from a brachyuran.

The *Lagenophrys* species reported here (Fig. 1, 2) possesses the generic characteristics of the type of the genus, *L. vaginocola* Stein, 1852. It differs from all other congeneric species in that it occurs on a marine brachyuran host. It further differs from *L. eupagarus* Kellicott, 1894, the only other species of the genus reported from a marine crab (the anomuran *Eupagarus*), in longest diameter of lorica (present species 57μ; *L. eupagarus* about 40μ). Further morphological and morphometric comparisons of the species with other congeneric species will be published elsewhere.

Species of the stalked peritrich genus *Epistylis* have been reported and described as epibionts from molluscs, arthropods, fish, and amphibians. Members of this genus demonstrate less rigid host specificity than do species of *Lagenophrys* (Nenninger, 1948). The determination of the specific taxonomic position of *Epistylis* species from the blue crab awaits further study.

The question of whether or not these peritrichs, particularly the space-consuming *Lagenophrys,* contribute to the death of crabs in shedding or holding tanks should be considered. Beaven and Truitt (1939) gave a number of possible causes of crab mortality in shedding tanks at Crisfield, Maryland. They reported that the holding of "green" crabs for extended periods to induce shedding was the greatest single factor contributing to high mortality. They did not suggest that another organism such as a parasite or commensal could have contributed to these mortalities. Twenty blue crabs, held in running sea water for several months (June–August, 1965) in a small tank (36″ x 24″ x 12″) at Franklin City, Virginia, began to die suddenly (within three days all were dead) when water temperatures reached their maximum (27–30°C) in August. The gills of four of nine crabs which were examined revealed extremely high numbers of *Lagenophrys*—higher concentrations than were found on the gills of crabs fresh from Chesapeake Bay. Large areas of the gill lamellae of three crabs from this tank were completely covered by *Lagenophrys* (Fig. 3). Many of these peritrichs were undergoing binary fission, the method of rapid proliferation for this genus. Coker (1901), who reported on the commensal barnacle *Dichelaspis* on the gills of the blue crab, stated: "Those crabs whose gills are heavily burdened with *Dichelaspis* have less vitality; their movements are sluggish and they are the first to die when brought into the laboratory. This reduction of vitality is not an evidence of real





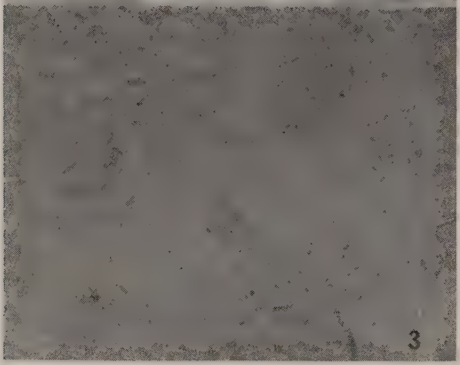


Fig. 1: *Lagenophrys* from blue crab (dorsal view). Stained with Heidenhain's iron hematoxylin. LA, lips of aperture; L, lorica; A, aperture of lorica; P, portion of peristomial or buccal cavity; Ma, macronucleus. (Scale of ten microns for both 1 and 2).

Fig. 2: *Lagenophrys,* ciliature of buccal cavity visible (dorsal view). C, cilia within buccal cavity; L, lorica.

Fig. 3: Individuals of *Lagenophrys* (unstained) in heavy concentration on surface of lamella from blue crab.

TABLE 1. Prevalence of ciliates on blue crabs at different localities. (August 1965)

Area sampled	Number of crabs examined	Crabs with ciliates: *Epistylis* only	*Lagenophrys* only	Both *Epistylis* and *Lagenophrys*	Crabs without ciliates
Chincoteague Bay, Va. (from Franklin City holding tanks, but originally from Chincoteague Bay)	9	4	3	1	1
Crisfield, Md. (from bay)	4	1	0	1	2
Toddville, Md. (from Toddville holding tanks)	7	0	5	2	0
Lower Fishing Bay, Md.	3	0	2	1	0
Upper Fishing Bay, Md.	3	0	2	1	0
Hooper Straits, Md.	3	0	3	0	0
Tred Avon River, Md.	12	1	5	0	6
Totals	41	6	20	6	9

parasitism, but may be explained by the fact that when the cirripeds are present in large numbers much of the gill surface is occupied, gill lamellae are fastened together, and the respiratory current retarded by them, and the barnacles have first chance at the water. The health of the host being thus impaired, much harm results indirectly to it, in that it is rendered less able to contend with its enemies or to escape their attacks". A similar situation could exist for blue crabs held in tanks and infested with the ciliates. The increase in numbers of epibionts, combined with possible infections of endoparasites, lowered oxygen tension in the warm water, crowding, and mechanical injury, may have contributed to a general anoxia in the crabs. Controlled experiments are needed to demonstrate further the role that these peritrichs play in crab mortalities.

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Sporulation of Minchinia nelsoni (Haplosporida, Haplosporidiidae) in Crassostrea virginica (Gmelin)

Abstract. Minchinia nelsoni, *which Haskin, Stauber, and Mackin found in connective tissue and digestive diverticula of the American oyster, is characterized by a distinct peripheral endosome in its plasmodial and spore nuclei and by spores of unique dimension (7.5 by 5.4 μ). This species is believed to be the etiologic agent, formerly reported as "MSX," responsible for extensive oyster mortalities along the Middle Atlantic Coast.*

Plasmodial stages of a haplosporidian parasite were found in oysters from the Middle Atlantic States. The organism was designated "MSX" (multinucleate sphere X). Since the discovery of the organism, studies of its life history, pathology, and epizootiology have been made (*1*). Plasmodial stages of this organism have been described and named *Minchinia nelsoni* by Haskin, Stauber, and Mackin (*2*). The organism is believed to be the pathogen responsible for "Delaware Bay Disease" (*1*) which has caused extensive oyster mortalities since 1957 along the Middle Atlantic Coast of the United States, particularly in the more saline (greater than 15 parts per thousand) estuarine waters of Delaware and Chesapeake bays.

In our studies of the distribution, prevalence, and pathological manifestations of this and other shellfish parasites, we have sampled oyster grounds from several areas in Chesapeake Bay for the past 6 years (*3*). Recently, prespore and spore stages of a haplosporidian parasite were found. We consider these stages to be part of the life cycle of *Minchinia nelsoni* in the oyster.

Spores and prespore stages were found in July 1965 in 12 of 266 oysters from Chincoteague Bay, the Manokin River, and Tangier Sound on the eastern shore of Chesapeake Bay. Sporocysts and spores were first observed in fresh-stained and unstained squash preparations of connective tissue and digestive diverticula of live oysters that were refrigerated at 5°C for 1 to 3 weeks. The squash preparations were stained either with toluidine blue (0.5 percent aqueous) or with Quensel's stain (*4*); other preparations were fixed in Davidson's fixative (*5*) and stained with iron hematoxylin. Remaining portions of the oysters were fixed in Davidson's fixative, sectioned, and stained with iron hematoxylin or with Harris' hematoxylin–Ziehl's fuchsin-eosin (*6*). Thirty fresh mature sporocysts and 200 fresh spores were measured. Spores were studied in detail, since their morphology presented important diagnostic characteristics of the genus *Minchinia* (*7*). Descriptions were based on fresh squashes and on sections stained with iron hematoxylin. All drawings were made with the aid of a camera lucida; measurements are in microns. Photomicrographs were made of fresh and fixed sporocysts and spores.

In the plasmodial stages (Fig. 1*A*) the organism is generally between and intimately associated with connective tissues of body, gills, and mantle; it is also between and displaces epithelial cells of the digestive diverticula. It is rarely intracellular. The shape is variable, but usually spheroid, 4 to 25 μ in greatest width. The organisms contain varying numbers of spherical nuclei, 1.5 to 2.0 μ in diameter. Each interphase nucleus contains a small endosome at, or near, nuclear membrane.

In the prespore stages, at the onset of sporulation, small plasmodia (Fig. 1*B*) and their nuclei increase in size preceding karyokinesis. Nuclear division (Fig. 1*C*) continues after the nuclei in the enlarged plasmodia have increased in size approximately threefold to fourfold. A conspicuous bar or spindle ("Kernstab" of Jirovec) (*8*) appears within the nuclear membrane; the compact endosome becomes associated with the spindle and divides. The

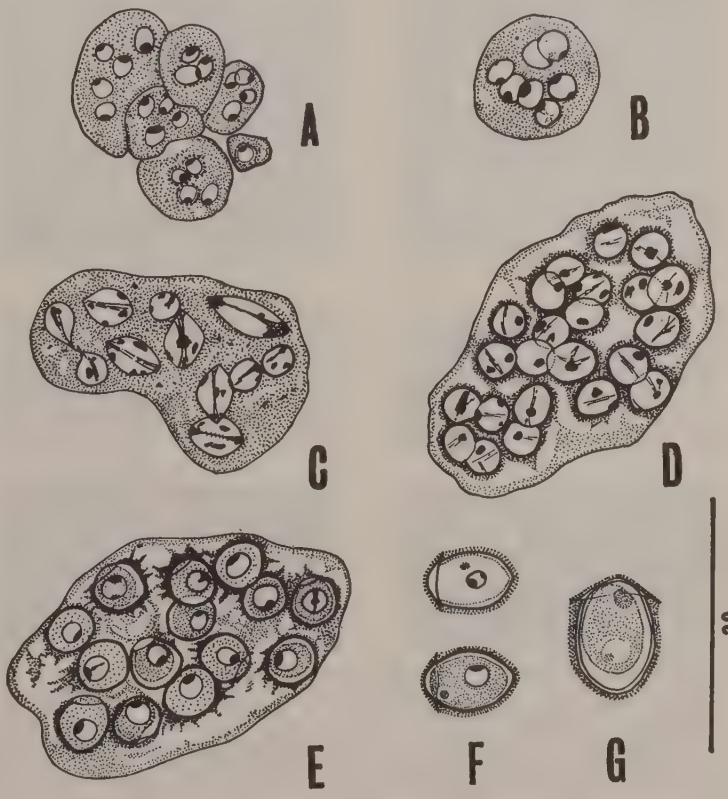

Fig. 1. Prespore and spore stages of *M. nelsoni*. *A*, Multinucleate plasmodia from connective tissue. *B*, Plasmodium with enlarged nuclei. *C*, Nuclear division within enlarged sporont. *D*, Sporont containing sporoblasts. *E*, Early sporocyst. *F*, Fixed and stained spores. *G*, Fresh spore. Measurements are in microns.

daughter nuclei (Figs. 1*D* and 2*A*), produced through karyokinesis, are still relatively large (3 to 4 μ), but in subsequent stages the size diminishes.

Sporonts (18 to 30 μ) formed after nuclear division contain the developing sporoblasts (Figs. 1*D* and 2*A*). Cytoplasmic condensation is apparent around the 3- to 4-μ sporoblast nuclei. The nuclei often possess remnants of the spindle. Sporoblasts rarely contain more than one nucleus. Nuclei are larger in early sporoblasts than in the more advanced. The reconstituted endosome is often adjacent to, or near, the nuclear membrane.

Early sporocysts (28 to 54 μ) are usually filled with a variable number of incompletely formed spores (Figs. 1*E* and 2*B*). Developing spores (6 to 8 μ) are round, with remnants of cytoplasm attached to the outside spore wall. An orifice is often apparent, but fully formed opercula are rare at this stage. Nuclei (1.5 to 2.0 μ) are smaller than those in sporoblasts. Remnants of a spindle are still present in a few nuclei.

Definitive sporocysts (28 to 54 μ) contain from 8 to about 50 spores, and rarely more (Fig. 2*D*). Sporulation is rare in the oyster, but when present, sporocysts are almost exclusively in the epithelium of the digestive diverticula. The oysters which contained sporocysts were 6 to 10 cm long, had orange to white diverticula, and were in poor condition. Histologically, the hosts showed extremely heavy plasmodial infection and a strong pathologic response.

The length of spores range from 5.3 to 10.7 μ and the width from 4.8 to 7.5 μ; modal size is 7.5 by 5.4 μ (Fig. 1, *F* and *G*, and Fig. 2, *E* and *F*). Fixation and staining cause about 10 percent shrinkage. The spore is surrounded by a refractive capsule (1 μ thick) without projections or appendages. It is rotund, with an operculum that extends laterally beyond the margin of the orifice to the margin of the capsule. The operculum is approximately 1 μ high. The wall is birefringent in fresh spores and opaque in optical section when stained (Fig. 1*F*). Sporoplasm is uninucleate and has a darkly staining spherule in various positions relative to the nucleus. The sporoplasm is apparently attached to the inner spore wall at or near the orifice. Upon maturing it becomes acid-fast, only partially fills the spore case, and the spherule disappears. The spore nucleus is small (1.5 to 2.0 μ) and has a peripheral endosome of identical appearance to those in smaller plasmodia (Fig. 1, *A* and *F*, and Fig. 2, *B* and *C*).

In addition to *Minchinia nelsoni*, two haplosporidians occur in oysters. One is an undescribed hyperparasite of the trematode *Bucephalus* (*9*); the other is a known species, *Minchinia costalis* (Wood and Andrews, 1962) (*1*).

The *Bucephalus* hyperparasite cannot be considered congeneric with *M. nelsoni* because it does not possess a spore operculum that originates from the capsule (*7*). Furthermore, stages of *M. nelsoni* have not been found in *Bucephalus* tissues in mixed infections. The trematode and particularly its hyperparasite occur rarely even in areas where *M. nelsoni* is abundant.

The spore of *M. nelsoni* is much larger than the spore of *M. costalis* (3.09 by 2.58 μ). The endosome of the interphase nucleus is always near or adjacent to the nuclear membrane and very distinct in *M. nelsoni*, but is often less distinct and usually not peripheral in *M. costalis*. Sporulation in *M. nelsoni* occurs in the epithelia of the terminal lobes of the digestive diverticula, whereas in *M. costalis* it occurs throughout the tissues. Another significant difference between *M. nelsoni* and *M. costalis* is the lack of antigenic similarity between the two species as found by Barrow and Taylor (*10*) with a fluorescent-antibody technique.

The remaining eight species in the genus *Minchinia* differ from *M. nelsoni* in the following aspects.

1) *M. chitonis* (Lankester, 1885) (*7, 11*) has capsular spore projections and a central nucleolus with radiating chromatin strands in the spore nucleus. Reported only from chitons.

2) *M. limnodrili* (Granata, 1913) (*7, 12*) has a reticulated spore nu-

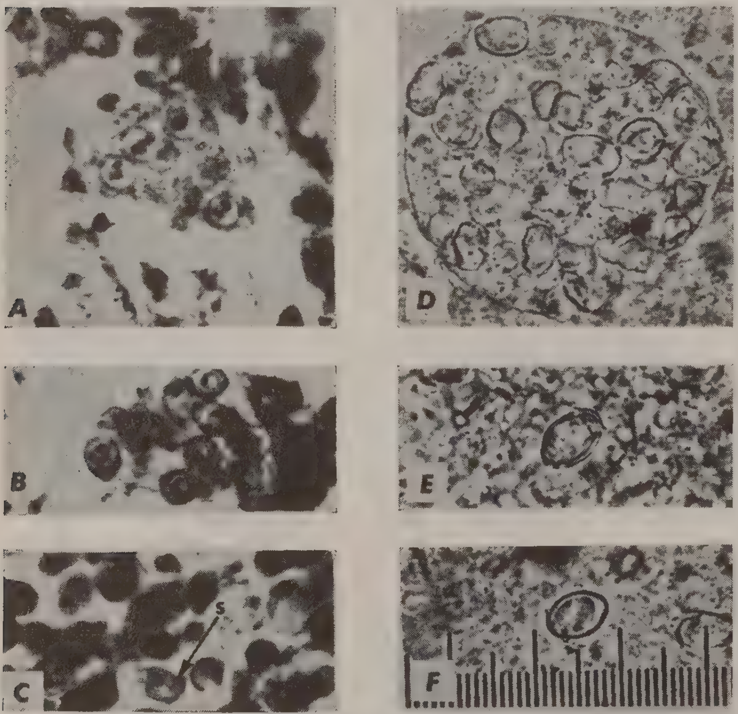

Fig. 2. *A*, Early sporont. *B*, Immature spores showing characteristic nucleus, opercula not yet formed. *C*, Maturing and mature operculate spores. Lighter-stained spore exhibits operculum, nucleus, and spherule (*s* arrow). *D*, Sporocyst in vivo. *E*, Spore in vivo, capsule and operculum in focus. *F*, Spore in vivo, wall and sporoplasm in focus. Nucleus and spherule visible. *A*, *B*, and *C* were stained with iron hematoxylin; *D*, *E*, and *F* show fresh material. Scale is the same for all photomicrographs; 1 micrometer unit equals 1 μ.

cleus and is reported from the fresh-water annelid *Limnodrilus udekemianus*.

3) *M. nemertis* (Debaisieux, 1919) (*7, 13*) has a spore with an excentric nucleolus and a conical operculum. It is found in the nemertean *Lineus bilineatus*.

4) *M. cernosvitovi* (Jirovec, 1936) (*7, 8*) has a central chromatin mass in the spore nucleus and was described from the fresh-water oligochaete *Opistocysta flagellum*.

5) *M. dentali* (Arvy, 1949) (*7, 14*) has a spore with a conical operculum and is found in the scaphopod *Dentalium* from Europe.

6) The spore of *M. pickfordae* (Barrow, 1961) (*7, 15*) possesses a collar and an excentric nucleolus and is found in fresh-water snails.

7) *M. louisiana* Sprague 1963 (*16*) has a larger spore than *M. nelsoni* and 3 to 4 peripheral chromatin granules in the nucleus. It was described from one specimen of the mud crab, *Panopeus herbstii*.

8) *M. ascidiarum* (Duboscq and Harrant, 1923) (*17*) has a central or slightly excentric nucleolus in its spore nuclei and was described from the ascidian *Amaroucium proliferum*.

Association of spores with vegetative stages formerly known only by the cryptic label "MSX" provides information about the sequence of life-cycle stages of *Minchinia nelsoni* in the oyster and further strengthens the placing by Haskin *et al.* of the organism in the genus *Minchinia*. However, the possibility of an alternate or intermediate host has not been eliminated, and spores identified in this study may provide workers with another stage to be used in future experiments on transmission. Such experiments and the determination of ecological conditions necessary for sporulation should enhance understanding of the epizootiology of this serious disease of American oysters.

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18. We thank Dr. J. H. Barrow of Hiram College and Dr. C. J. Sindermann, Biological Laboratory, for discussion and cooperation, and B. Taylor, G. Kidder, G. Ward, Mrs. V. Liddell, and Mrs. C. Sullivan for technical assistance. Personnel of the Maryland Department of Chesapeake Bay Affairs provided us with oyster samples.

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On the Application of Immunological Techniques in Geographic Group Studies of Atlantic Sea Herring, *Clupea harengus* [1,2]

I. NEUTRALIZATION OF IMMUNE PRECIPITINS AS AN AID TO HERRING SERUM ANALYSIS BY IMMUNOELECTROPHORESIS

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ABSTRACT The sera of Atlantic sea herring, collected from 13 contiguous oceanic locations, were analyzed by immunoelectrophoresis for precipitinogen differences. An immune serum (rabbit) against the sera from each location was required. Electrophoretic characteristics suitable for identifying the geographic origins of herring sera were not detected. Immune serum aliquots were therefore individually neutralized with undiluted or one of a series of dilutions of herring serum from each geographic location prior to analysis. The use of undiluted serum resulted in complete precipitin neutralization regardless of its origin. Equivalent dilutions of each serum resulted in varying degrees of precipitin neutralization. This capacity of origin-separate precipitinogens appears to be related to the geographical distance separating the origins of immunizing and neutralizing sera, i.e., the greater the distance the higher the concentration necessary for equivalent neutralization. Sera of unknown origins can be related to sera from specific origins by comparison at equivalent dilutions for equivalent precipitin neutralization, providing they originate from the overall area sampled. Immunoelectrophoretic results are consistent regardless of sex, number of individuals contributing to the sample or the collection date. Herring precipitinogens are identified by comparison with the well-established mobilities of human precipitinogens and are discussed based on the frequency with which they are associated with geographic group differences.

The solution to long-standing problems of conservation and management associated with economically important marine organisms, including the Clupeidae, depends upon an understanding of their ecology as well as migratory and breeding habits. Occupying a major role in the ensuing studies, morphologists continue to identify species distinguishing characteristics. Separation of close relatives, however, becomes increasingly difficult, particularly with immature members. Consequently the role of serology in fishery research has received increasing attention (Bargetzi, '58; Cushing, '52, '56; Fine and Drilhon, '60; O'Rourke, '59, '60; Ridgway, '57, '62; Sindermann and Mairs, '59; and others) with impetus arising from the necessity to identify intraspecies groups and to determine their natural relationships and affinities.

Mairs and Sindermann ('62) have reported on a serological comparison of five species of clupeoids employing turbidimetric precipitin tests (Boyden and De Falco, '43), gel double diffusion analysis (Ouchterlony, '48), erythroctye (clupeoid) agglutination wtih absorbed antisera, and paper electrophoresis. Combined results indicate that alewives, *Alosa pseudoharengus,* and blueback herring, *Alosa aestivalis,* are serologically very similar; that shad, *Alosa sapidissima,* are closer to the alewife-blueback complex than menhaden, *Brevoortia tyrannus;* and that herring, *Clupea harengus,* are serologically remote from all. Having defined the "serological distances" between these clupeoids, such investigations provide a foundation for

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comparable studies on the existence and discreteness of intraspecies populations.

The present report and those of the series to follow present an extensive examination of sea herring serum, undertaken to (1) evaluate several immunological techniques seldom used (collectively) in investigations of this nature, and (2) to distinguish, if possible. intraspecific differences in serum soluble antigens. Pooled serum samples of herring were taken at specific oceanic locations with a portion of each utilized for rabbit immunization and the remainder for assay. The resulting antiherring sera were examined (individually), after reaction with electrophoretically separated serum of each location, for numbers and mobilities of immunoprecipitins, specificity (degree of cross reactivity) and neutralization (inhibiting) capacity. An attempt was then made to correlate rabbit immune responses with specific geographic groups.

MATERIALS AND METHODS

Collection and preparation of samples

Herring blood samples were withdrawn according to the method described by Perkins ('57), delivered into glass tubes, sealed and stored at + 4°C until clotted. Following decanting, centrifugation, and addition of sodium azide (0.1% w/v), the sera were transferred to vials and stored at − 20°C until tested. Thirteen oceanic locations were sampled (fig. 1) with collection extending from September, 1956 to April, 1964. Pooled samples consisted of 10 to 100 or more adult individuals col-

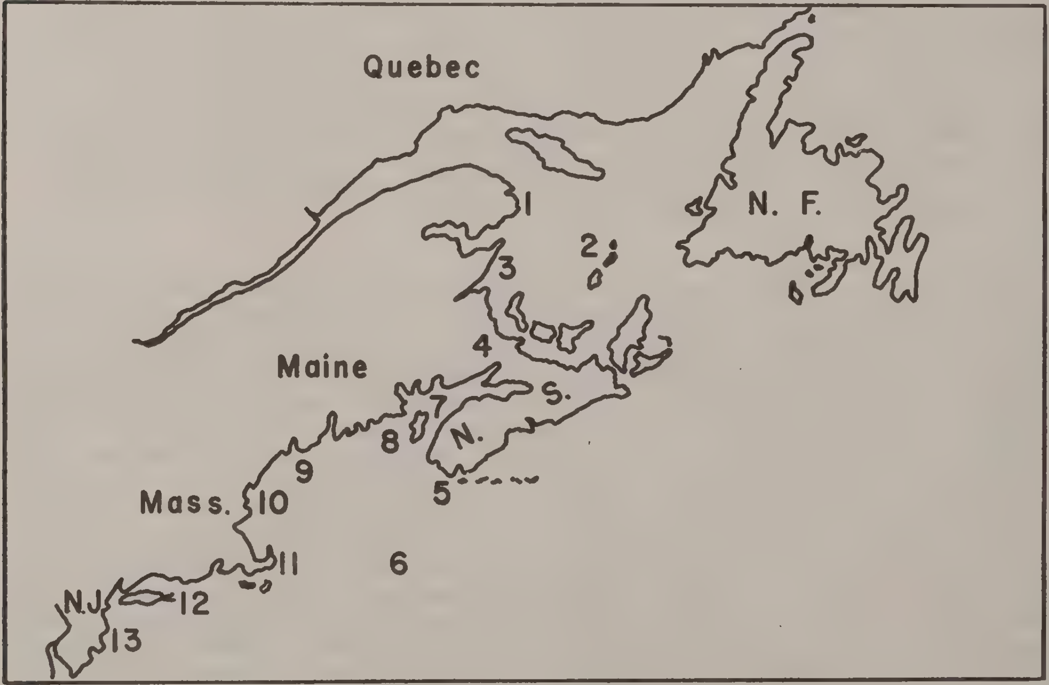


Fig. 1 Oceanic locations of herring sampled in this investigation.

1	Gaspé
2	Magland Islands
3	Richibucto
4	Shediac
5	Trinity Ledges
6	Georges Bank
7	Yarmouth Bar
8	Grand Manan
9	Cape Porpoise
10	Isle of Shoals
11	Provincetown
12	Stonington
13	Belford

lected at random. T.S. meter (Goldberg Refractometer — American Optical Company) determinations for protein concentration varied from 2.5% to 5.2%. Samples were standardized for protein concentration prior to assay. Care was taken to avoid repeated freezing and thawing of the samples.

Production of antisera

All herring antisera were produced in mature rabbits of either sex (table 1). Trial bleedings were taken from the ear and exsanguinations by cardiac puncture. Blood was allowed to clot for 24 hours at + 4°C before harvesting serum. Sodium azide (0.1% w/v) was added and 5 ml aliquots were stored at — 20°C until tested.

Method of testing

Immunoelectrophoresis, first described by Grabar and Williams ('53), was carried out on an apparatus designed by the investigator according to the following conditions:

a. *Electrolyte*. Veronal buffer, prepared by adding 0.92 gm barbituric acid plus 5.15 gm sodium barbitol per liter of distilled water; stored at + 4°C (pH 8.6, 0.025 μ).

b. *Supporting medium*. Special Agar — Noble (Difco Laboratories, Detroit, Michigan), 1% (w/v) in electrolyte. Stored at + 4°C in 100 ml aliquots (volume required per assay).

c. *Apparatus* (fig. 2). The 2 electrolyte and 2 agar wicks (Whatman — 3 mm) measured, respectively, 40 cm × 20 cm and 2 cm × 20 cm. The electrophoretic dish (1/8 inch plexiglass) measured 21.5 cm × 21.5 cm × 2 cm. The electrophoretic plate (single weight glass) measured 18 cm × 19 cm × 0.4 cm and was placed in the dish prior to adding the agar. It served as a support for removing the agar-precipitate complex for photography. The base (plexiglass) dimensions are not critical providing the dish rests in a level position with the electrodes (coiled platinum wire) extended beyond the 21.5 cm limit.

d. *Electrophoresis*. Desired resolution was achieved in approximately 4 hours (+ 4°C) at a constant voltage of 375v. The amperage ranged from 25 to 30 ma (Variable Voltage Power Supply, Model No. PS-3, Heathkit Company, Ann Arbor, Michigan). A constant voltage transformer was placed in series (Model No. 20-13-060, Solo Electric Company, Elk Grove, Illinois).

"Curing" of the agar was found perferable to immediate use, and for this purpose each dish was sealed in foil and stored for

TABLE 1

Immunization schedule

Animal no.	Inoculum	Volume/ injection	Inoculated on day	Trial bled on day	Exsanguinated on day
BH-1	Gaspé herring serum (pooled)	0.5 ml	1–4 (IV[1])	9	43
			12, 13 (SC[2])	11	(BH-1—BH-6)
To BH-15	Each remaining serum, 2–13 (fig. 1), was treated in like manner		14 (IV)	19	
			24, 25 (SC)	31	38
			26 (IV)	34	(BH-7—BH-15)
			36 (SC)	42	
			37 (IV)		
			(12 inoculations)		

[1] Intravenous.

[2] Subcutaneous.

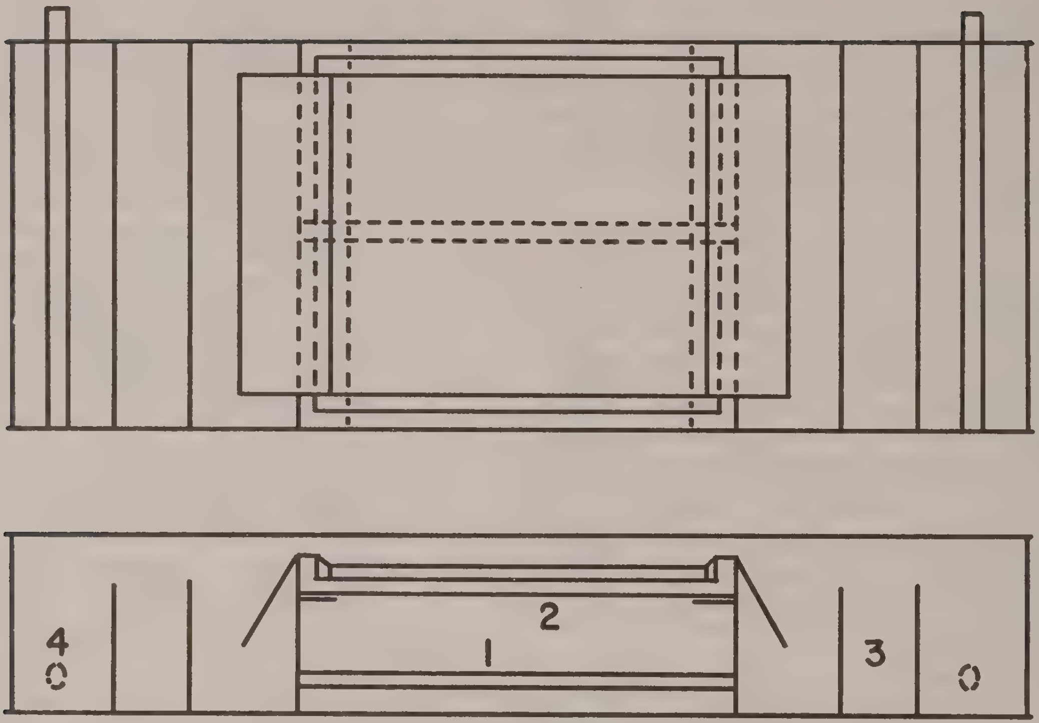


Fig. 2 Immunoelectrophoresis dish and base

1 Hydrostatic bridge	2 Dish
3 Reservoir	4 Electrode

24 to 48 hours (+ 4°C) immediately prior to phoresis. Antigen wells were cut with a No. 1 cork borer and cleared with a fine gauge hypodermic needle. Antibody troughs were cut with a scalpel and cleared with forceps. A template was used to insure that uniform dimensions were obtained for and between the wells and troughs. The electrolyte reservoirs were filled with the hydrostatic bridge opened to insure osmotic equilibrium (closed during phoresis). The entire apparatus was allowed to equilibrate (+ 4°C, 375v), serum samples (0.1 ml) were placed in designated wells and the phoresis continued for 4 hours plus or minus 5 to 10 minutes. To minimize migration differences between analyses, the actual duration of each was adjusted so that a 50% mixture of bovine serum albumin and 1% bromphenol blue progressed to an anodal point equidistant from respective antigen wells. Precipitates were readily observable after 48 to 72 hours incubation at + 4°C.

To determine if herring sera (1) contain precipitinogens specific for their origin which are (2) identifiable by different precipitin neutralizing capacities, antisera were treated as follows: equal volumes of antiserum (undiluted) and herring serum, standardized for protein concentration and serially diluted in buffer to 1:10, 1:20 and 1:40, were mixed in separate tubes and allowed to incubate at room temperature for 30 minutes prior to phoresis termination. This procedure was essential since the use of undiluted herring serum, regardless of origin, resulted in complete antibody neutralization. All neutralized antisera were compared with the same antisera diluted 1:2 (buffer). Precipitation differences were, therefore, attributed to antibody neutralization rather than dilution.

RESULTS

Precipitates observed prior to antiserum neutralization

Typical results are shown in figure 3. Ten oceanic locations are represented employing an antiserum to one (anti-Gaspé BH-1). Figure 4 schematically indicates the established precipitinogen mobilities of human serum and those collectively observed with herring sera. Table 2 summarizes immunoelectrophoretic results indicating the human precipitinogens for which those of herring sera exhibited similar mobility.

TABLE 2

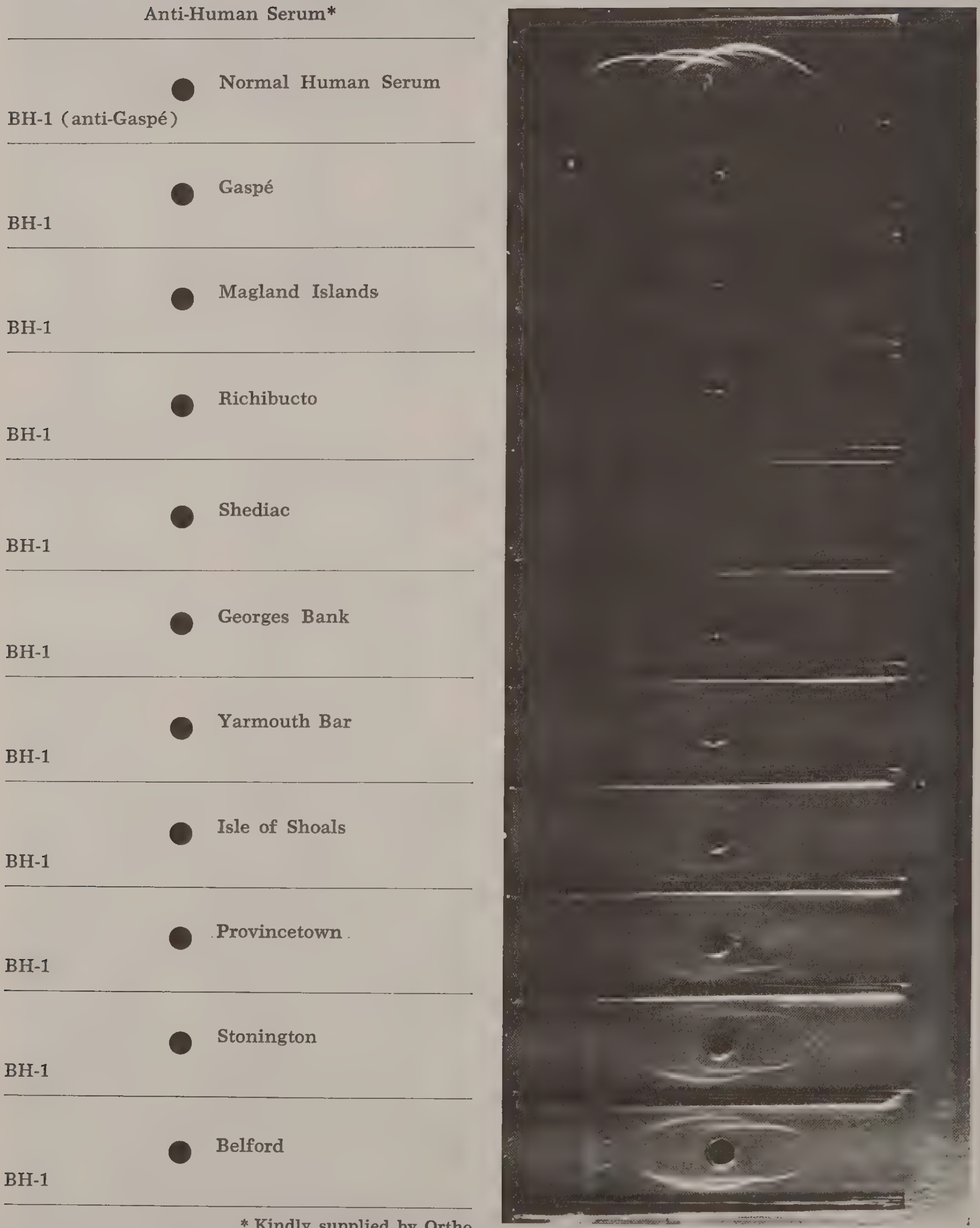
Precipitates observed with rabbit antiserum no. BH-1 [1]

Test serum		Pool size	Antiserum no. BH-1 (anti-Gaspé) Trial bled on day			
Location	Date		9	19	34	42
Gaspé	9/56	100+	α_2	α_2, H, IgM α_1, S, IgA		
	9/57	30			α_2, H, IgM (F) α_1, S	α_2, H, IgM α_1, S, IgA
Magland Islands	5/58	25	— [2]	—	α_2, H, IgM α_1, S, IgA (F)	Same as day 34 — stronger development
Grand Manan	9/57	100+	α_2	α_2, H, α_1 (F)		
	4/58	30			α_2, H, IgM α_1, S	α_2, H, IgM α_1, S, IgA
Yarmouth Bar	9/57	100+	α_2	α_2, H, IgM α_1, S, IgA		
Georges Bank	10/58	100+	—	—	α_2, H, IgM α_1, S, IgA	Same as day 34 — stronger development
Cape Porpoise	11/59	30	—	—	α_2, H, IgM α_1, S, IgA	Same as day 34 — stronger development
Provincetown	5/58	100+	α_2, α_1 (F)	α_2, H, IgM α_1, S		
	10/58				α_2, H(F) IgM α_1, S	α_2, H, IgM α_1, S, IgA
Belford	4/64	30	—	—	α_2, H, IgM α_1, S, IgA (Alb?)	Same as day 34 — stronger development
Shediac	5/63	10	α_2	α_2, H, IgM (F) α_1, S	α_2, H, IgM α_1, S, IgA	Same as day 34 — stronger development
Richibucto	5/58	25	—	—	α_2, H, IgM α_1, S, IgA	Same as day 34 — stronger development
Isle of Shoals	?/58	10	α_2	—	α_2, H, IgM α_1, S, IgA	Same as day 34 — stronger development
Stonington	4/64	26	α_2	—	α_2, H, IgM α_1, S, IgA	Same as day 34 — stronger development

Abbreviations are as follows: α_2, alpha$_2$ glycoprotein; α_1, alpha$_1$ glycoprotein; *H*, haptoglobin; *S*, siderophilin (transferrin); *IgM* (γ_{1M}, 19S, slow, B_2M) macroglobulin; *IgA*, (fast, γ_{1A}, B_2A) globulin; (*F*), trace or faint precipitin formation; (*Alb?*), component with a mobility questionably similar to human albumin.

[1] Results for antisera BH-2 through BH-15 are essentially the same. The occasional differences observed were not of the magnitude necessary for identifying sample origins.

[2] Not done.


Anti-Human Serum*
Normal Human Serum
BH-1 (anti-Gaspé)
Gaspé
BH-1
Magland Islands
BH-1
Richibucto
BH-1
Shediac
BH-1
Georges Bank
BH-1
Yarmouth Bar
BH-1
Isle of Shoals
BH-1
Provincetown
BH-1
Stonington
BH-1
Belford
BH-1

* Kindly supplied by Ortho Pharmaceutical Corporation, Raritan, New Jersey.

Fig. 3 Immunoelectrophoresis.

Antisera recovered on days 9 and 11 (table 1) react with herring precipitinogens similar in mobility to human alpha$_2$ glycoprotein and/or siderophilin. Increase to the maximum number of precipitates observed with each serum-antiserum system is essentially the same regardless of the immunizing serum origin. Further examination (day 11–42) reveals that all herring sera tested are devoid of a precipitinogen similar in mobility to human IgG (or at least that concentration required for precipitin stimulation). Approximately 85% of these sera are also devoid of a precipitinogen of similar mobility to human albumin. The remaining 15% contain a fast anodal component of questionable similarity to human albumin. Several of these sera were treated (twice) with 50% saturated $(NH_4)_2SO_4$. The supernatants,[4] recovered by centrifugation and dialyzed against buffer, were tested with homologous antisera (exsanguinates) by the method of Ouchterlony ('48). Repeated attempts to observe precipitation proved negative. The mobility of the fast anodal precipitinogen was, therefore, considered dissimilar to human albumin. It could not be associated with the remaining human precipitinogens identified in figure 4.

Degrees of precipitation were periodically observed among herring sera when each was tested with any one antiserum, regardless of the extent of immunization. However, these differences were not sufficient for serum identification with a specific geographic origin. It is important to note that although heterologous[5] sera generally contain the same precipitinogens when tested with equivalent bleedings of each antiserum, those present in homologous serum always appear (precipitate) first, a point not revealed by figures 3 and 5. In a number of tests, homologous serum can also be indentified by the precipitinogens present, containing those similar in mobility to human alpha$_2$ glycopro-

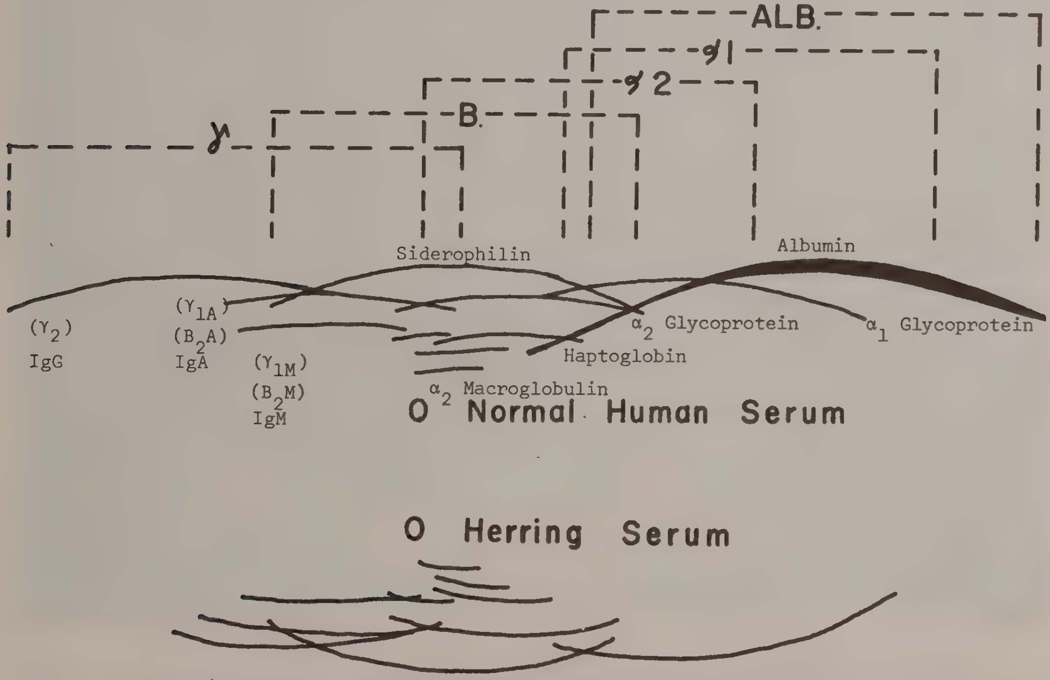


Fig. 4 Schematic representation of precipitinogen mobilities obtained with normal human serum and herring sera.

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[4] The supernatant from $(NH_4)_2SO_4$ precipitation will contain albumin plus other proteins and probably small amounts of the original globulins.

[5] In this context "heterologous" refers to samples of herring sera other than those used for antibody stimulation.

Explanation of Figure 5

BH-1 (anti-Gaspé) 1:2	Anti-human Serum
● Gaspé BH-1	● Normal Human Serum BH-1 (anti-Gaspé) + Gaspé at 1:10
● Magland Islands BH-1	● Gaspé BH-1 + Magland Islands at 1:10
● Grand Manan BH-1	● Gaspé BH-1 + Grand Manan at 1:10
● Georges Bank BH-1	● Gaspé BH-1 + Georges Bank at 1:10
● Cape Porpoise BH-1	● Gaspé BH-1 + Cape Porpoise at 1:10
● Provincetown BH-1	● Gaspé BH-1 + Provincetown at 1:10
● Belford BH-1	● Gaspé BH-1 + Belford at 1:10
● Shediac BH-1	● Gaspé BH-1 + Shediac at 1:10
● Richibucto BH-1	● Gaspé BH-1 + Richibucto at 1:10
● Isle of Shoals BH-1	● Gaspé BH-1 + Isle of Shoals at 1:10
● Stonington BH-1	● Gaspé BH-1 + Stonington at 1:10

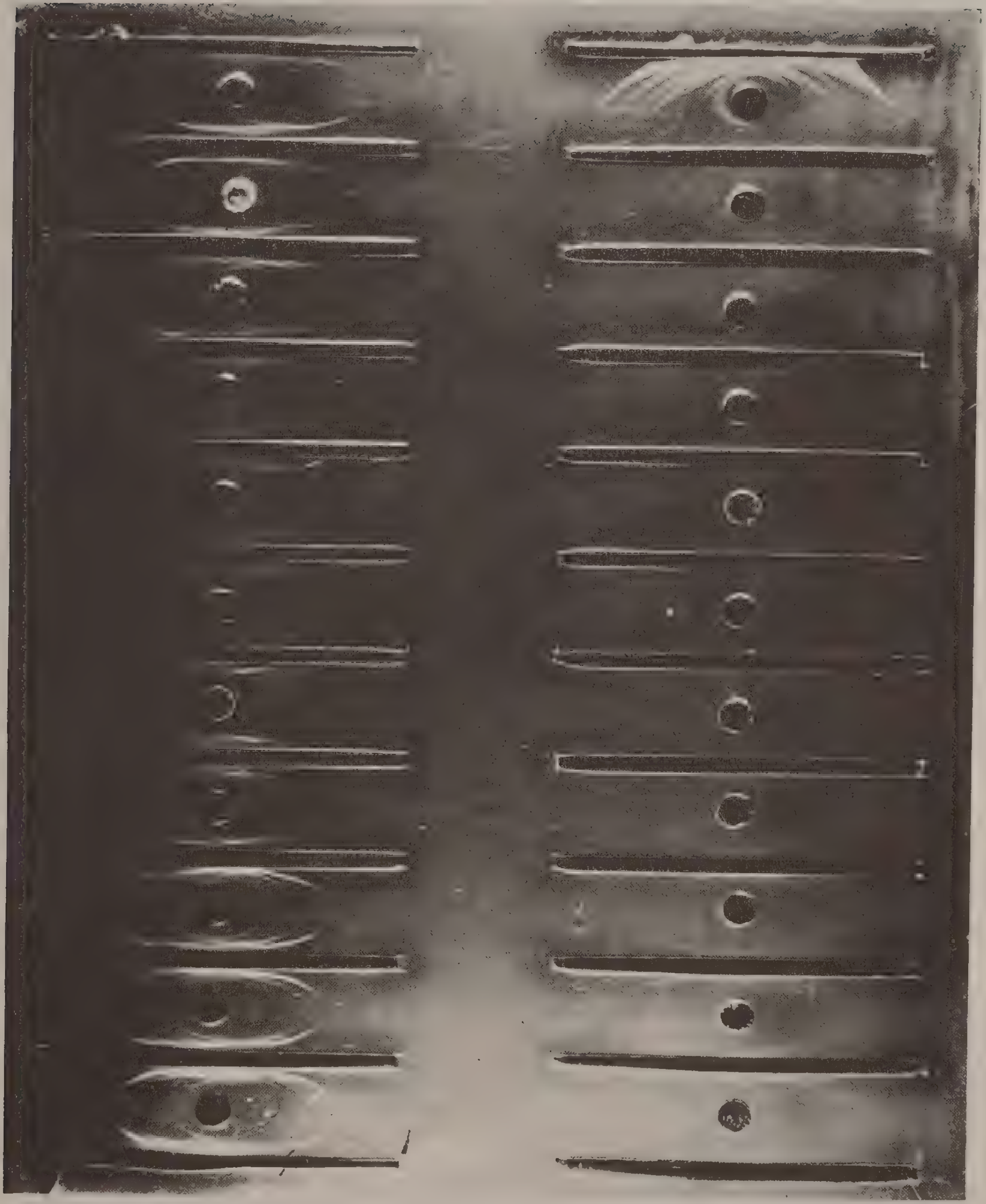

Fig. 5 Immunoelectrophoresis.

tein, siderophilin and/or $alpha_1$ glycoprotein when precipitated with day 9 antiserum. Heterologous sera exhibit a single precipitinogen similar in mobility to $alpha_2$ glycoprotein. Under these conditions, when testing several sera (pools) of unknown origin with an equivalent antiserum, one may exhibit greater avidity and complexity of precipitates. Such observations suggest origin identity or close geographic proximity to that of the immunizing serum. However, identification with specific geographic groups becomes essentially impossible with increased immunization (day 9–43). These observations apply to sera regardless of pool size or collection date.

Precipitates observed after antiserum neutralization

Typical results are shown in figure 5 with ten oceanic locations represented, employing an antiserum to one (anti-Gaspé BH-1). Troughs to the left were charged with untreated antiserum and those to the right with the same antiserum divided into 11 aliquots, each having been neutralized as previously described. Unfortunately, the resolution of human serum illustrated in figure 4 is not matched with the precipitates shown in figure 5 (uppermost right) due to excessive diffusion. Resolution identical to that illustrated was achieved by delayed application of anti-human serum (18–24 hours after the anti-herring serum). Table 3 summarizes the immunoelectrophoretic results indicating the human precipitinogens for which those of herring serum exhibited similar mobility.

Evidence for the existence of geographic groups within the species is obtained by neutralizing antiserum prior to immunoelectrophoresis. Equivalent neutralization (of antisera harvested at the same intervals) requires a lower concentration of homologous serum. The ability to identify samples with their origins was confirmed by comparing the number of precipitates present after neutralizing each available antiserum (table 1) with equivalent concentrations of each serum. Under these test conditions samples of unknown origin can be identified through a process of elimination by substitution for sera of known origins (providing the unknown origins are within the overall area assayed). Comparison of all test systems suggests that the degree of neutralization is directly proportional to the geographic distance separating serum origins, i.e., the greater the geographical distance between immunizing and neutralizing sera, the higher the concentration of the latter required for equivalent antibody neutralization (figs. 1 and 5). Reciprocal testing provides perfect agreement.

Initial precipitation is observed in regions of similar mobility to human $alpha_2$ glycoprotein and/or siderophilin and also in these same regions after antiserum neutralization with the lowest concentrations of herring sera utilized. The corresponding herring precipitinogens are, therefore, regardless of origin, primary stimulators of antibody and consequently responsible for the greatest degree of precipitin inhibition. These observations apply to sera regardless of pool size or collection date.

DISCUSSION

The immunoelectrophoretic results reported in this paper, utilizing neutralized antiserum, demonstrate the utility of a specialized technique for the study of intraspecies serum soluble antigens. Ten precipitinogens were detected (fig. 4) although no single herring — anti-herring system exhibited all of them. The number of precipitates (arcs) observed is dependent upon the presence and concentration of specific precipitins in the antiserum employed. Prolonged immunization was considered unnecessary, however, as no significant difference in the number of precipitates occurred between day 34 and 42 (table 2).

Herring precipitinogens were identified by their similarity to known human precipitinogen mobilities. Similarity in any other manner is not implied. Of particular interest is the absence, in all herring sera tested, of a precipitinogen similar to human IgG. Approximately 85% of these sera are also devoid of a precipitinogen similar to human albumin. The possibility that selective deterioration during storage is responsible for the absence of either is unlikely since sera tested within 48 hours of collection are also devoid. Such evidence

TABLE 3

Precipitates observed with neutralized rabbit antisera

Test serum used for neutralization			Antiserum			
Location and date	Pool size	Dilution	BH-1 (anti-Gaspé)	BH-3 (anti-Provincetown)	BH-6 (anti-Grand Manan)	BH-10 (anti-Belford)
			Trial bled on day			
			42	42	42	38
Gaspé 9/57	30	1:10	CN	α_2 (F), S (F)	α_2 (F)	α_2 (F), S
		1:20	CN	α_2, S, α_1	α_2 (F)	α_2, S, IgM(F), α_1(F)
		1:40	CN	α_2, S, IgM (F), α_1, H (Alb?)	α_2, S (F)	α_2, S, IgM, α_1
Magland Islands 5/58	25	1:10	CN	α_2 (F), IgM (F), α_1 (F)	α_2 (F)	α_2, S, IgM (F)
		1:20	α_2 (F), S, α_1 (F)	α_2, S, IgM, α_1	α_2, S (F)	α_2, S, IgM, α_1 (F)
		1:40	α_2, S, α_1 (F)	α_2, S, IgM, α_1, (Alb?)	α_2, S, IgM (F)	α_2, S, IgM, α_1
Grand Manan 4/58	30	1:10	α_2 (F)	α_2 (F), S (F)	CN	α_2 (F), S (F)
		1:20	α_2	α_2, S	CN	α_2, S
		1:40	α_2	α_2, S, α_1 (F)	CN	α_2, S, IgM, α_1 (F)
Georges Bank 5/58	100+	1:10	α_2, S (F)	α_2 (F), S (F)	α_2 (F)	α_2, S (F), IgM (F)
		1:20	α_2, S (F)	α_2, S	α_2 (F)	α_2, S, IgM, α_1 (F)
		1:40	α_2, S	α_2, S, α_1 (F)	α_2 (F), S (F)	α_2, S, IgM, α_1
Cape Porpoise 11/59	30	1:10	α_2, S (F)	S (F)	α_2 (F)	α_2 (F), S (F), IgM (F)
		1:20	α_2, S (F)	α_2, S (F)	α_2 (F)	α_2, S, IgM, α_1 (F)
		1:40	α_2, S	α_2, S, α_1 (F)	α_2 (F), S (F)	α_2, S, IgM, α_1
Provincetown 10/58	25	1:10	α_2, S, IgM (F)	S (F)	α_2 (F), S (F)	α_2 (F), S (F), IgM (F)
		1:20	α_2, S, IgM	S (F)	α_2, S (F)	α_2, S, IgM (F)
		1:40	α_2, S, IgM	α_2 (F), S (F)	α_2, S, IgM (F)	α_2, S, IgM
Belford 4/64	30	1:10	α_2 (F), IgM (F)	S (F), IgM (F)	α_2 (F), S	CN
		1:20	α_2, S, IgM (F)	α_2 (F), S	α_2, S (F)	CN
		1:40	α_2, S, IgM	α_2 (F), S	α_2, S	α_2 (F), S (F), α_1 (F)
Shediac 5/63	10	1:10	α_2 (F), S (F)	α_2 (F), S, IgM	α_2, S (F), IgM (F)	α_2 (F), S (F)
		1:20	α_2, S, IgM (F)	α_2 (F), S, IgM, α_1 (F)	α_2, S (F), IgM (F)	α_2, S, IgM (F)
		1:40	α_2, S, IgM (F)	α_2, S, IgM, α_1 (F)	α_2, S, IgM	α_2, S, IgM, (Alb?)
Richibucto 5/58	25	1:10	S (F), IgM (F)	α_2 (F), S, IgM	α_2(F), S(F)	α_2 (F), S (F), IgM (F)
		1:20	S, IgM (F)	α_2, S, IgM	α_2,S(F), IgM(F)	α_2, S, IgM (F), α_1 (F)
		1:40	S, IgM	α_2, S, IgM	α_2, S, IgM	α_2, S, IgM, α_1
Isle of Shoals ?/58	26	1:10	α_2(F), S, IgM (F)	α_2 (F), S, IgM (F)	α_2 (F), S (F), IgM (F)	α_2 (F), S (F), IgM (F)
		1:20	α_2, S, IgM (F)	α_2 (F), S, IgM	α_2, S, IgM	α_2 (F), S, IgM
		1:40	α_2, S, IgM,α_1 (F)	α_2 S, IgM, α_1 (F)	α_2, S, IgM, α_1 (F)	α_2, S, IgM
Stonington 4/64	26	1:10	α_2 (F), S, IgM (F)	S (F)	α_2 (F), S (F), IgM (F)	α_2 (F), S (F), IgM (F)
		1:20	α_2, S, IgM	α_2 (F), S	α_2, S, IgM	α_2, S, IgM (F)
		1:40	α_2, S, IgM,α_1 (F)	α_2, S, α_1 (F)	α_2, S, IgM	α_2, S, IgM

Abbreviations are as follows: α_2, alpha$_2$ glycoprotein; α_1, alpha$_1$ glycoprotein; *H*, haptoglobin; *S*, siderophilin (transferrin); *IgM*, (19S, γ_1M, slow, B_2M) macroglobulin); *IgA*, (fast, γ_1A, B_2A) globulin; *CN*, complete neutralization; (*F*), trace or faint precipitin formation; (*Alb?*), component with a mobility questionably similar to human albumin.

points to the necessity of evaluating comparative disease resistance levels of herring and other marine species known to contain IgG and/or albumin similar components.

The alpha$_2$ glycoprotein similar precipitinogen is least frequently associated with geographic group differences (table 3). Excluding homologous test systems, it is the most commonly observed component regardless of the neutralizing serum origin or dilution. Conversely, the IgA and haptoglobin similar precipitinogens were not observed in any of the neutralized test systems. Those components routinely associated with geographic group differences are similar in mobility to siderophilin, alpha$_1$ glycoprotein and IgM. Utilizing equivalent dilutions, the presence and intensity of their corresponding precipitates appear to be directly proportional to the distance separating the neutralizing serum origins.

As previously indicated, the use of undiluted herring serum, regardless of origin, resulted in complete precipitin neutralization. Consequently, qualitative differences could not be detected. A decision regarding the actual existence of such differences would be more feasible after determining the capacity of herring to produce isoprecipitins. Nevertheless, the results obtained are due to the relative concentration of soluble antigens within the pooled samples, i.e., sea herring contain quantitative serum variations related to their origins. This may be evidence of genetic subdivision since the results are consistent for specific geographic areas and reproducible over an extensive sampling period.

Mature female birds and fish are known to contain serum antigens not present in males or immature females (Sasaki, '32; Vanstone et al., '55; Ridgway et al., '62; and others). The use of pooled samples could, therefore, render the preceding interpretations doubtful. To clarify such a possibility, several hundred individual adult sera, also collected at random, were tested by the immune (indirect) hemagglutination technique of Boyden ('51), to be discussed later in this series. Theoretically 50% of these individuals would be female as would be the case with the pooled samples. The individuals do not vary significantly from their corresponding pools when tested through a twenty tube serial dilution series. In addition, all are capable of complete antibody neutralization when utilized undiluted. Since the individual sera mimic the results obtained with pooled sera of the same origin, regardless of sex, the original interpretations seem justifiable.

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Bathymetric Distribution of Fish in the Apostle Islands Region, Lake Superior

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Bathymetric Distribution of Fish in the Apostle Islands Region, Lake Superior

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ABSTRACT

Records of seasonal and "all-season" (April–December) bathymetric distribution are given for 17 species of fish taken in bottom trawls and experimental gill nets fished on the bottom in 1958–63 in the Apostle Islands region of Lake Superior. The data are based on catches from 578 trawl tows at 2–59 fathoms and 301,900 linear feet of gill nets fished at 2–89 fathoms. Size of the fish varied widely among different species from the same gear and the same species from different gears. Seasonal differences in depth distribution were greatest for lake trout, bloaters, round whitefish, and older smelt, which exhibited an inshore movement in the summer and fall, and for longnose suckers, which migrated to deeper water with progress of the seasons. The all-season bathymetric distributions varied considerably among species. Round whitefish, 0- and I-group smelt, longnose suckers, ninespine sticklebacks, and johnny darters were most abundant at < 10 fathoms. Concentrations of lake trout, lake herring, lake whitefish, older smelt, trout-perch, and burbot were greatest at 10–29 fathoms. Pygmy whitefish were most common at 30–39 fathoms, bloaters and spoonhead sculpins at 40–49 fathoms, and shortjaw ciscoes, slimy sculpins, and fourhorn sculpins at 50–59 fathoms. The kiyi was most abundant at 70–79 fathoms.

INTRODUCTION

Understanding the life histories and interrelations of fishes requires information on their bathymetric distribution. Despite the importance of this knowledge, few major studies of the bathymetric distribution of Great Lakes fish have been undertaken, probably because researchers lacked vessels and gear for the large-scale fishing required. The commercial fishery has provided limited records for some species, but fishermen tend to fish only the depths at which catches are best. Only through extensive fishing with experimental gear at various depths and seasons can adequate knowledge be gained on the depth distribution of most species.

The earliest substantial records on depth distributions for Great Lakes fish are those of Koelz (1929) for several species of coregonines. His data were based almost entirely on observations of the commercial fishery. The Bureau of Fisheries R/V *Fulmar* obtained considerable information in 1930–32 on the bathymetric distribution of several species in Lake Michigan. Some of these data were included in papers by Deason (1939) for cottids, Jobes (1943) for shortnose cisco,[1] Hile and Deason (1947) for the kiyi, Jobes (1949a) for the longjaw cisco, Jobes (1949b) for the bloater, and Van Oosten and Eschmeyer (1956) for lake trout. Other observations on the bathymetric distribution of Great Lakes fish were those of Van Oosten, Hile, and Jobes (1946) for lake whitefish, lake trout, burbot, walleye, white sucker, and longnose sucker in Lake Huron, and for lake whitefish, lake trout, and burbot in Lake Michigan. Smith (1956) described the distribution of lake herring in Green Bay, and Pritchard (1931) and Stone (1947) made observations on the depth distribution of ciscoes (*Coregonus* spp.) in Lake Ontario.

The only studies on Lake Superior which include information on bathymetric distributions are those of Eschmeyer and Bailey (1955) for the pygmy whitefish, Eschmeyer (1956) for young lake trout, and Dryer and Beil (1965) for lake herring. The present study, based on data from trawls and gill nets, expands the observations to species common in the Apostle Islands region.

MATERIALS AND METHODS

The data for the present study were accumulated in 1958–63 through experimental fishing in western Lake Superior by the Bureau of Commercial Fisheries R/V *Siscowet.* Although the work was directed primarily to several studies of the abundance, distribution, and movement of juvenile lake trout, data also were collected on other species.

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[1] A list of common and scientific names of fish mentioned in this paper appears in the section on "Materials and Methods."

The fishing gear consisted of otter trawls and experimental gill nets. The trawls were semiballoon, with a 31-foot headrope, 2- to 2½-inch-mesh (stretched measure) cotton body, and ½-inch-mesh cod end. Trawls were dragged on the bottom along the contour lines, usually for 15 minutes, at a speed of 3 miles per hour. Catch records from shorter or longer trawl tows were adjusted to 15 minutes. A total of 578 tows was made at 2–59 fathoms in various locations in the Apostle Islands region (Table 1, Figure 1).

The experimental nylon gill nets were 150 to 300 feet long and 6 feet deep; a gang included as many as nine mesh sizes from 1 to 5 inches (stretched measure as manufactured) by ½-inch intervals. The nets of various meshes were randomly distributed within the gangs. The net length and depth of water were recorded for each mesh size as it was set, and the catches were recorded by individual net as the gangs were lifted. A total of 301,900 linear feet of gill nets was fished at 2–89 fathoms at various locations in 1958–63 (Table 2, Figure 1).

The data from gill nets were compiled in terms of catch per 1,000 feet of net lifted adjusted for equal lengths of each mesh unless otherwise stated, but regardless of the length of time the nets were fished. Although the total catch undoubtedly was affected by the fishing time, general conclusions on the bathymetric distribution were affected little because nearly all sets in 1958–62 were 1 night out, all in 1963 were 2 nights out,[2] and a wide range of depths was fished each period.

TABLE 1.—*Number of 15-minute trawl tows made in the Apostle Islands region according to year and depth of water*

Year	Depth of water (fathoms)						Total
	<10	10–19	20–29	30–39	40–49	50–59	
1958	9	6	5	5	2	2	29
1959	9	30	17	5	3	0	64
1960	1	21	37	6	2	2	69
1961	5	31	45	7	0	2	90
1962	3	26	124	21	2	0	176
1963	6	15	124	5	0	0	150
Total	33	129	352	49	9	6	578

The data for 1958–63 were combined because no annual differences in distribution by depth were detected. The abundance of certain species may have fluctuated during the 6-year period, but the relative numbers at different depths remained nearly constant from year to year.

Details on collections of various species for the study of bathymetric distribution are given in Table 3. The data are combined regardless of year, season, or depth of water. The average lengths for shortjaw cisco, round whitefish, burbot, trout-perch, and fourhorn sculpin taken in trawls have been omitted because the number of fish measured was extremely small.

Although the data are scanty or lacking for some species, the records of Table 3 give a general idea of the size of the fish of various species included in the study. The average lengths were undoubtedly affected by the se-

TABLE 2.—*Length of experimental gill nets lifted in 1958–63 according to mesh size and depth of water*
[Thousands of feet]

Mesh size[1] (inches)	Depth of water (fathoms)									Total
	<10	10–19	20–29	30–39	40–49	50–59	60–69	70–79	80–89	
1	1.5	4.1	7.8	1.2	1.7	1.7	0.6	0.5	0.5	19.6
1½	1.5	5.7	10.5	2.1	2.4	3.0	0.9	0.9	0.6	27.6
2	1.5	16.3	22.4	2.4	2.7	3.0	0.9	0.9	0.6	50.7
2½	0.9	11.9	20.8	1.5	2.4	2.7	0.9	0.9	0.6	42.6
3	0.6	15.7	21.2	2.4	2.1	3.0	0.9	0.9	0.6	47.4
3½	0.6	11.4	16.5	1.8	2.1	3.0	0.9	0.9	0.6	37.8
4	0.6	8.7	12.3	1.5	2.1	2.4	0.9	0.9	0.6	30.0
4½	0.6	5.4	9.0	1.8	2.1	2.4	0.9	0.9	0.6	23.7
5	0.6	4.8	8.7	1.5	2.1	2.4	0.9	0.9	0.6	22.5
Total	8.4	84.0	129.2	16.2	19.7	23.6	7.8	7.7	5.3	301.9

[1] Stretched measure.

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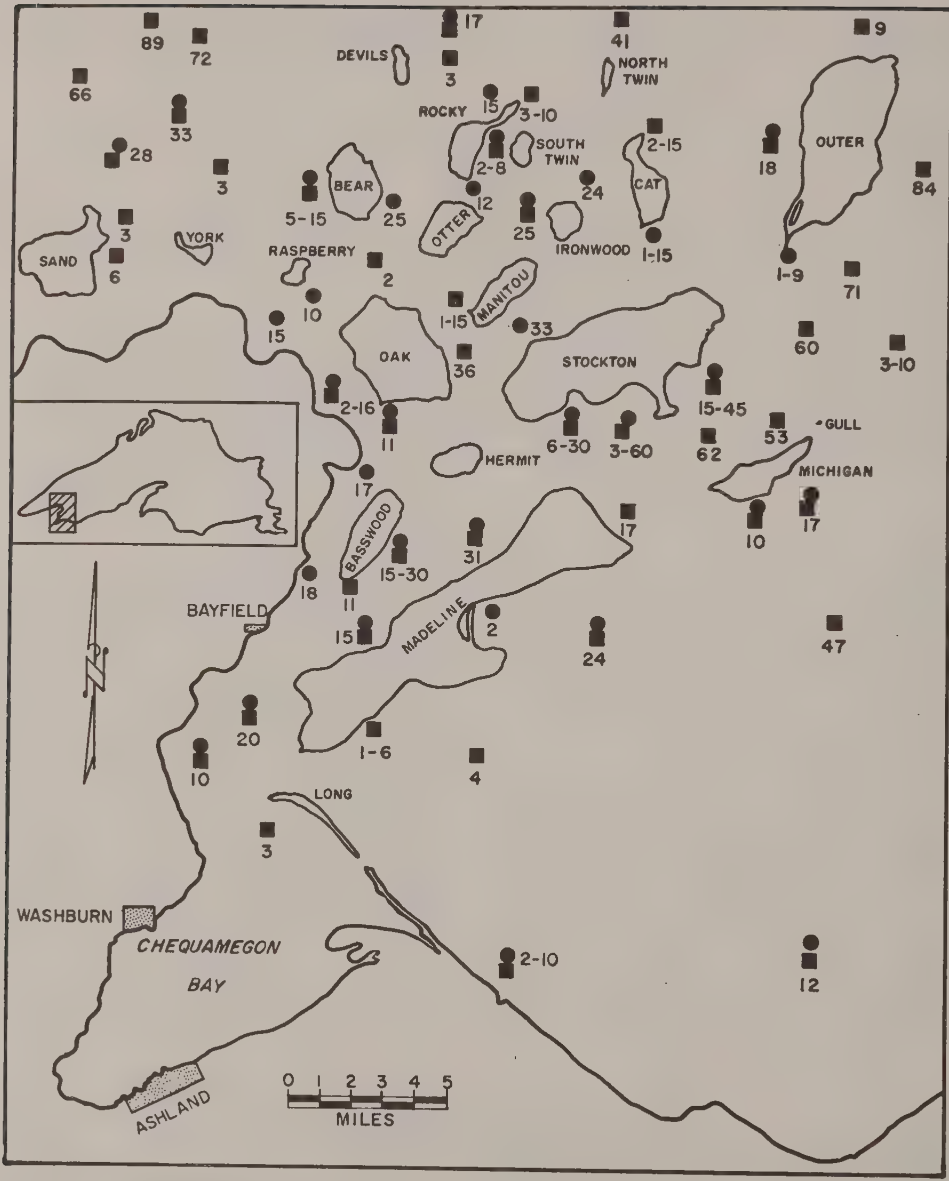
[2] According to Hile (1962), the catch from gill nets fished 2 nights averaged less than 20% greater than the catch of nets fished 1 night.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NORTH TWIN
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CAT
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BEAR
5-15
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OTTER
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IRONWOOD
1-15
RASPBERRY
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MANITOU
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OAK
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STOCKTON
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GULL
HERMIT
MICHIGAN
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BASSWOOD
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MADELINE
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WASHBURN
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MILES

FIGURE 1.—Apostle Islands region of Lake Superior. The dots represent trawl stations, and the squares gill net stations. The numbers indicate depths in fathoms.

lective actions of the gears. The mean lengths and length ranges varied widely among different species taken from the same gear and between fish of the same species collected in different gears. The mean lengths of fish from trawls ranged from 2.4 inches for slimy sculpin to 10.2 inches for lake whitefish. The average lengths of fish from gill nets ranged from 7.3 inches for II-group and older smelt to 15.0 inches for burbot.

TABLE 3.—*The number, average length, and range in length of various species caught in trawls and gill nets in the Apostle Islands region, 1958–63*

Species and gear[1]	Number captured	Number measured	Total length (inches)	
			Average	Range[2]
Lake trout				
Trawl	3,940	3,892	8.1	3.2–16.7
Gill net	1,511	1,399	13.1	5.7–28.2
Lake whitefish				
Trawl	241	146	10.2	4.2–18.2
Gill net	549	522	11.4	5.7–19.2
Lake herring				
Gill net	1,210	477	11.4	5.7–18.2
Bloater				
Trawl	6,420	385	8.9	4.2–11.7
Gill net	13,242	1,451	9.3	5.2–12.2
Kiyi				
Gill net	481	210	9.7	7.2–11.2
Shortjaw cisco				
Gill net	1,482	508	9.8	7.2–14.7
Round whitefish				
Gill net	1,047	950	11.1	5.7–18.7
Pygmy whitefish				
Trawl	770	316	4.6	1.7– 6.7
Smelt (0 and I group)[4]				
Trawl	6,081	1,703	2.6	1.2– 5.2
Smelt (II group and older)[4]				
Trawl	17,262	503	6.2	4.2– 9.2
Gill net	2,151	635	7.3	5.2–11.2
Longnose sucker				
Gill net	1,862	[3]515	14.1	7.2–18.7
Burbot				
Gill net	593	[3]398	15.0	10.2–19.2
Ninespine stickleback				
Trawl	29,911	[3]316	2.8	1.7– 3.2
Slimy sculpin				
Trawl	12,900	[3]223	2.4	1.2– 3.7
Spoonhead sculpin				
Trawl	149	[3] 54	3.0	1.7– 4.2

[1] Measurements not available for additional species captured in the following numbers: trout-perch, 8,285; johnny darter, 405; fourhorn sculpin, 215.

[2] Midpoints of 0.5-inch intervals.

[3] Includes measurements of fish taken in 1964.

[4] See text for explanation of the division of smelt.

Age determinations by Bailey (1964) made possible the separation of 0- and I-group smelt from older fish. The spring and early-summer records for young smelt were based entirely on I-group fish. When young-of-the-year smelt appeared in the late-summer and early-fall catches, the I-group fish were recorded with the older fish and the records for the young smelt were based on 0-group fish.

The trawls and gill nets captured an occasional alewife, white sucker, yellow perch, walleye, rainbow trout, and brown trout. The numbers taken, however, were far too small to indicate distribution.

All of the references to fishes in this study are by common name. The following common and scientific names are from the list published by the American Fisheries Society (1960):

Common name	*Scientific name*
Alewife	*Alosa pseudoharengus*
Lake trout	*Salvelinus namaycush*
Brown trout	*Salmo trutta*
Rainbow trout	*Salmo gairdneri*
Lake whitefish	*Coregonus clupeaformis*
Lake herring	*Coregonus artedii*
Longjaw cisco	*Coregonus alpenae*
Bloater	*Coregonus hoyi*
Kiyi	*Coregonus kiyi*
Shortnose cisco	*Coregonus reighardi*
Shortjaw cisco	*Coregonus zenithicus*
Round whitefish	*Prosopium cylindraceum*
Pygmy whitefish	*Prosopium coulteri*
American smelt	*Osmerus mordax*
White sucker	*Catostomus commersoni*
Longnose sucker	*Catostomus catostomus*
Burbot	*Lota lota*
Ninespine stickleback	*Pungitius pungitius*
Trout-perch	*Percopsis omiscomaycus*
Johnny darter	*Estheostoma nigrum*
Walleye	*Stizostedion vitreum vitreum*
Yellow perch	*Perca flavescens*
Slimy sculpin	*Cottus cognatus*
Spoonhead sculpin	*Cottus ricei*
Fourhorn sculpin	*Myoxocephalus quadricornis*

The records for fish captured in trawls (Table 4) and gill nets (Table 5) include data on seasonal and "all-season" (April–December) depth distribution. Seasonal differences were not apparent for some species, and for others the data were inadequate to show possible changes. The records for these fish, therefore, are given only in terms of all-season averages. Catches were grouped by 10-fathom intervals, from < 10 to 59 fathoms for trawls and < 10 to 89 fathoms for gill nets. Figures 2 to 4 are based on percentages of the all-season average catches listed in Tables 4 and 5.

The seasons of Tables 4 and 5 are based on periods of different thermal conditions in the lake. In the spring (26 April–15 July), the water in the Apostle Islands region is generally homothermous, although surface temperatures in shallow areas may reach 60 F in early July. A shallow thermocline (the bottom of which rarely extends below 12 fathoms) is normally present in the summer (16 July–15 September), and surface temperatures frequently reach 70 F in protected areas among the Islands. The water begins to cool in early fall (mid-September), and by mid-October it is again homothermous but at

TABLE 4.—*The average number of fish of various species caught per 15-minute trawl tow at different depths in the Apostle Islands region, during various seasons in 1958–63*

[Spring = April 1–July 15; summer = July 16–September 15; fall = September 16–December 13. Percentage of the all-season catch in parentheses]

Species and season	Depth of water (fathoms)					
	<10	10–19	20–29	30–39	40–49	50–59
Lake trout						
Spring	0.0	3.4	9.1	3.0	0.0	0.0
Summer	0.0	2.7	11.8	0.4	0.0	0.0
Fall	0.0	4.3	9.4	1.3	0.0	0.0
All seasons	0.0	3.5	10.1	1.6	0.0	0.0
	(0.0)	(23.0)	(66.5)	(10.5)	(0.0)	(0.0)
Lake whitefish						
All seasons	0.0	0.6	0.4	0.1	0.0	0.0
	(0.0)	(54.5)	(36.4)	(9.1)	(0.0)	(0.0)
Bloater						
Spring	0.0	1.5	10.7	20.8	22.3	20.3
Summer	0.0	9.6	15.0	21.6	37.0	15.0
Fall	0.0	5.2	32.4	19.0	40.2	22.0
All seasons	0.0	5.4	19.3	20.4	33.1	19.1
	(0.0)	(5.5)	(19.8)	(21.0)	(34.1)	(19.6)
Pygmy whitefish						
All seasons	0.0	0.3	1.7	2.4	1.1	0.0
	(0.0)	(5.5)	(30.9)	(43.6)	(20.0)	(0.0)
Smelt (0 and I group)						
Spring	84.8	51.2	1.1	0.6	0.0	0.0
Summer	13.3	2.3	[1]0.0	0.0	0.0	0.0
Fall	42.1	17.4	5.0	1.7	0.0	0.0
All seasons	46.7	23.6	2.0	0.8	0.0	0.0
	(63.9)	(32.3)	(2.7)	(1.1)	(0.0)	(0.0)
Smelt (II group and older)						
Spring	0.2	41.6	35.5	45.7	0.0	0.0
Summer	0.0	16.1	18.8	3.2	0.0	0.0
Fall	0.0	41.8	34.3	26.4	0.0	0.0
All seasons	0.1	33.1	29.5	25.1	0.0	0.0
	(0.1)	(37.7)	(33.6)	(28.6)	(0.0)	(0.0)
Ninespine stickleback						
All seasons	251.6	39.5	53.3	35.7	104.2	151.7
	(39.5)	(6.2)	(8.4)	(5.6)	(16.4)	(23.9)
Trout-perch						
All seasons	7.2	35.5	6.8	21.7	1.2	0.0
	(9.9)	(49.0)	(9.4)	(30.0)	(1.7)	(0.0)
Johnny darter						
All seasons	10.7	0.4	0.0	0.0	0.0	0.0
	(96.4)	(3.6)	(0.0)	(0.0)	(0.0)	(0.0)
Slimy sculpin						
All seasons	14.7	27.4	18.1	23.2	64.7	131.7
	(5.3)	(9.8)	(6.5)	(8.3)	(23.1)	(47.0)
Spoonhead sculpin						
All seasons	0.0	0.0	0.1	0.7	7.2	2.5
	(0.0)	(0.0)	(1.0)	(6.7)	(68.5)	(23.8)
Fourhorn sculpin						
All seasons	0.0	0.0	0.0	0.0	0.5	35.0
	(0.0)	(0.0)	(0.0)	(0.0)	(1.4)	(98.6)
Number of tows						
Spring	12	63	151	27	3	3
Summer	9	24	87	10	1	2
Fall	12	42	114	12	5	1
Total	33	129	352	49	9	6

[1] Less than 0.05.

slightly higher temperatures than in the spring. Earliest and latest fishing in any year were 26 April and 13 December.

The trawl data (Table 4) are presented in terms of the average catch per 15-minute tow by depth, season, and species. For gill nets (Table 5), the unweighted average catch per 1,000 feet was computed by season, depth, and species for each of the nine mesh sizes. Seasonal data are given only for depths at which each of the nine meshes was fished. The records for smelt older than the I group are based only on catches in 1-inch-mesh nets.

BATHYMETRIC DISTRIBUTION

Lake trout

Small lake trout from trawls were most abundant at 20–29 fathoms in all seasons but were most common at this depth in the summer (Table 4). Their relative abundance at 30–39 fathoms was highest in the spring and in the fall at 10–19 fathoms. Trawls cap-

TABLE 5.—*The average number of fish of various species caught per 1,000 feet of gill nets at different depths in the Apostle Islands region, during various seasons in 1958–63*
[Spring = April 26–July 15; summer = July 16–September 15; fall = September 16–December 13. Percentage of the all-season catch in parentheses]

Species and season	Depth of water (fathoms)								
	<10	10–19	20–29	30–39	40–49	50–59	60–69	70–79	80–89
Lake trout									
Spring	0.0	3.1	5.7	1.9	0.0	0.5	0.2	0.4	0.0
Summer	—	3.2	3.1	0.0	0.1	0.0	—	—	—
Fall	0.4	4.9	3.1	—	0.0	—	0.0	0.0	—
All seasons	0.2	3.7	4.0	1.0	[1]0.0	0.3	0.1	0.2	0.0
	(2.1)	(38.9)	(42.1)	(10.5)	(0.0)	(3.2)	(1.1)	(2.1)	(0.0)
Lake whitefish									
All seasons	0.2	1.5	1.6	0.3	0.0	0.0	0.0	0.0	0.0
	(5.6)	(41.7)	(44.4)	(8.3)	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)
Lake herring									
Spring	1.9	3.4	4.3	1.7	0.6	1.3	0.6	0.7	0.6
Summer	—	3.3	4.7	0.4	1.6	0.9	—	—	—
Fall	1.5	9.8	4.2	—	0.0	—	0.0	0.7	—
All seasons	1.7	5.5	4.4	1.1	0.7	1.1	0.3	0.7	0.6
	(10.6)	(34.3)	(27.3)	(6.8)	(4.3)	(6.8)	(1.9)	(4.3)	(3.7)
Bloater									
Spring	0.0	2.4	18.7	90.6	128.6	85.8	43.6	17.4	5.6
Summer	—	3.1	30.0	39.4	56.0	69.8	—	—	—
Fall	0.0	22.3	76.5	—	132.5	—	22.2	4.1	—
All seasons	0.0	9.3	41.7	65.0	105.6	77.8	32.9	10.8	5.6
	(0.0)	(2.7)	(12.0)	(18.6)	(30.3)	(22.3)	(9.4)	(3.1)	(1.6)
Kiyi									
All seasons	0.0	0.0	0.1	0.5	0.5	4.6	14.4	17.1	16.1
	(0.0)	(0.0)	(0.2)	(0.9)	(0.9)	(8.6)	(27.0)	(32.2)	(30.2)
Shortjaw cisco									
Spring	0.0	0.8	2.5	8.3	10.2	14.5	16.5	2.0	2.8
Summer	—	0.3	2.1	12.6	5.7	7.5	—	—	—
Fall	0.0	0.7	4.0	—	13.7	—	2.2	0.7	—
All seasons	0.0	0.6	2.9	10.5	9.9	11.0	9.4	1.4	2:8
	(0.0)	(1.2)	(6.0)	(21.6)	(20.4)	(22.7)	(19.4)	(2.9)	(5.8)
Round whitefish									
Spring	20.9	21.1	0.7	0.1	0.0	0.0	0.0	0.0	0.0
Summer	—	1.5	0.4	0.0	0.0	0.0	—	—	—
Fall	26.5	8.1	0.5	—	0.0	—	0.0	0.0	—
All seasons	23.7	10.2	5.3	0.5	0.0	0.0	0.0	0.0	0.0
	(59.7)	(25.7)	(13.3)	(1.3)	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)
Smelt (II group and older)[2]									
Spring	203.3	113.8	131.7	48.6	0.0	3.0	2.2	0.0	0.0
Summer	2.2	41.3	161.9	233.3	104.8	0.0	—	—	—
Fall	125.0	215.0	176.4	—	26.7	0.0	0.0	0.0	—
All seasons	110.1	123.2	156.5	141.0	43.8	1.0	1.1	0.0	0.0
	(19.1)	(21.4)	(27.1)	(24.4)	(7.6)	(0.2)	(0.2)	(0.0)	(0.0)
Longnose sucker									
Spring	7.0	10.1	0.6	1.0	0.0	0.1	0.0	0.0	0.0
Summer	—	6.3	0.1	0.0	0.0	0.0	—	—	—
Fall	13.2	13.6	7.3	—	0.0	—	0.0	0.0	—
All seasons	10.1	10.0	2.7	0.5	0.0	[1]0.0	0.0	0.0	0.0
	(43.4)	(42.9)	(11.6)	(2.1)	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)
Burbot									
All seasons	0.7	2.4	1.6	0.9	0.6	0.4	0.4	0.0	0.0
	(10.0)	(34.2)	(22.9)	(12.9)	(8.6)	(5.7)	(5.7)	(0.0)	(0.0)
Feet of nets lifted[3]									
Spring	4.8	25.5	52.2	11.2	5.6	17.0	5.2	5.1	5.3
Summer	[4]0.5	22.9	37.1	5.0	11.5	6.6	0.0	0.0	0.0
Fall	3.6	35.6	39.9	0.0	2.6	[4]0.3	2.6	2.6	0.0
Total	8.4	84.0	129.2	16.2	19.7	23.6	7.8	7.7	5.3

[1] Less than 0.05.
[2] Based on catches of 1-inch-mesh nets only.
[3] In thousands of feet.
[4] 1-inch mesh only.

tured small lake trout only at depths of 10 to 39 fathoms (Figure 2).

The larger lake trout from gill nets (Table 5) were taken in greatest numbers at 20–29 fathoms in the spring, were nearly evenly distributed between 10 and 29 fathoms in the summer, and were most common at 10–19 fathoms in the fall. An occasional lake trout was caught in the spring at depths down to 70–79 fathoms. Although seasonal differences were small, there is some evidence that the lake trout moved from deep to shallow water with progress of the seasons. As in the trawl catches, however, lake trout were most common at 10–29 fathoms when data were combined for all seasons (Figure 2).

In other studies, Eschmeyer (1956) found that I- and II-group lake trout (3.5 to 9.2

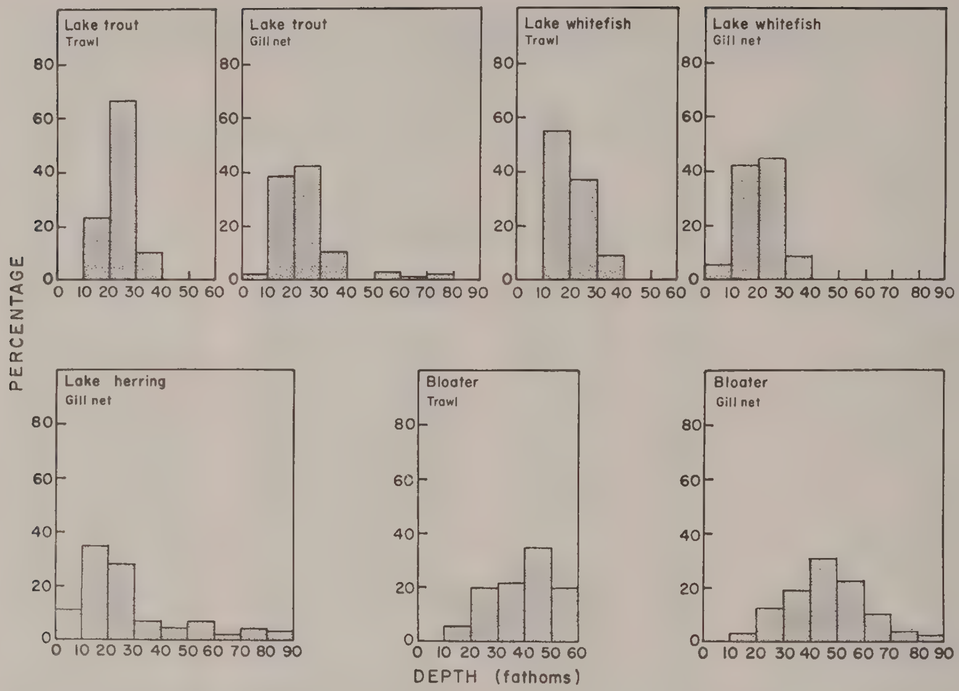

FIGURE 2.—The all-season average percentages of fish of various species captured per 15-minute trawl tow or per 1,000 feet of gill nets according to depth.

inches long) from trawls and gill nets were caught at 15–49 fathoms in Keweenaw Bay but were most plentiful at 20–34 fathoms. Van Oosten and Eschmeyer (1956) reported that juvenile lake trout (mostly 12 to 15 inches long) from small-mesh gill nets in Lake Michigan were most abundant at 40–49 fathoms in the south end of the lake and at 30–39 fathoms in the north end.

Lake whitefish

The number of lake whitefish captured by the R/V *Siscowet* was too small to provide information on seasonal changes in depth distribution. The records nevertheless give an idea of the all-season distribution of juvenile whitefish in the Apostle Islands region.

Nearly all the smaller lake whitefish from trawls (Table 4, Figure 2) were captured at 10–29 fathoms and none were taken above 10 or below 39 fathoms. The larger lake whitefish from gill nets (Table 5) were also mostly taken at 10–29 fathoms. A few were taken at < 10 fathoms but none were captured at depths below 39 fathoms (Figure 2).

Koelz (1929), who based his records on catches from pound and gill nets, reported for Lake Superior that most of the lake whitefish were taken at 20–35 fathoms in early spring, but as the season progressed the fish moved inshore. As the water warmed in early summer, the lake whitefish were scarce at all depths until fall, when schools returned to shoal areas to spawn. He stated that fishermen had reported lake whitefish during the summer at 60–70 fathoms in eastern Lake Superior. His records for the other Great Lakes were similar to those for Lake Superior: the lake whitefish migrated in early spring from relatively deep water to shoal areas, but as the water warmed the fish moved off the shoals. In the fall the lake whitefish returned to shallow water to spawn. Lake whitefish were rarely taken at depths greater than 35 fathoms.

Lake herring

Lake herring rarely were captured in trawls and were relatively scarce in gill nets at all depths and seasons, except in the fall when the largest catches were made at 10–19 fathoms. The species was most common at 20–29 fathoms in the spring and summer, and a few fish were taken at depths greater than 29 fathoms throughout the year. The all-season averages indicate that the lake herring was most common at 10–29 fathoms (Table 5, Figure 2).

The pelagic nature of the species undoubtedly accounts for the scanty catches in bottom nets. Dryer and Beil (1965) reported that the catch of lake herring from gill nets set on the bottom was small at all depths and periods except during the spawning season, when they were caught at depths ranging from 3 to 90 fathoms. Catches from floating and "oblique" nets suggested that lake herring were most common near the surface in early summer, but moved to deeper water as the surface water warmed in midsummer. In advance of spawning in early fall, the fish began to form large schools at depths above 20 fathoms.

Bloater

Bloaters from trawls (Table 4) were about evenly distributed between 30 and 59 fathoms in the spring and were most abundant at 40–49 fathoms in the summer and fall. The catches at 10–29 fathoms suggest that bloaters migrate to shallower water during the summer and fall.

The records from gill nets (Table 5) show that bloaters were most common at 40–49 fathoms in the spring and fall and at 50–59 fathoms in the summer. The catches from depths less than 30 fathoms also suggest an inshore movement in the summer and fall. Although summer and fall data are scanty at depths greater than 49 fathoms, the records suggest that the increase in abundance in shallower water is accompanied by a decrease in abundance in deeper water. The all-season averages for trawls and gill nets (Figure 2) indicate a progressive increase in abundance from 10–19 to 40–49 fathoms and a progressive decline at greater depths.

Koelz (1929) indicated that the bathymetric distribution of bloaters in Lake Superior ranged from 15 to 90 fathoms, but that they were most common at 35–50 fathoms. Bloaters were taken at depths as shallow as 15 fathoms only in the summer (which supports the above suggestion of an inshore movement during that season). On the west shore of Lake Michigan, bloaters were taken in the summer from pound nets set at 5 fathoms. Dryer, Erkkila, and Tetzloff (1965) reported that the occurrence of *Coregonus* (probably bloaters) in the stomachs of lake trout from depths less than 36 fathoms increased steadily from early spring to late fall.

Kiyi

The catches of kiyi were inadequate to show seasonal differences in distribution but the all-season averages indicate that they were absent at depths less than 20 fathoms and increased progressively in abundance down to 79 fathoms (Table 5, Figure 3). The slight decrease in the value at 80–89 fathoms may reflect an inadequate amount of fishing rather than the true distribution. Records of catches by the R/V *Siscowet* in deep waters near Isle Royale, Michigan, suggest that kiyi are abundant at 100 fathoms.

Koelz (1929) stated that except during the spawning season, the majority of kiyi were taken from 100 fathoms in Lake Superior and only rarely were they caught with bloaters.

Shortjaw cisco

Shortjaw ciscoes were most abundant at 60–69 fathoms in the spring, at 30–39 fathoms in the summer, and at 40–49 fathoms in the fall (Table 5). The all-season averages indicate the species to be widely distributed between 10 and 89 fathoms but most common at 30–69 fathoms (Figure 3).

Koelz (1929) also found a wide range in bathymetric distribution for shortjaw ciscoes: 11–100 fathoms in Lake Superior, 12–90 fathoms in Lake Michigan, and 14–100 fathoms in Lake Huron.

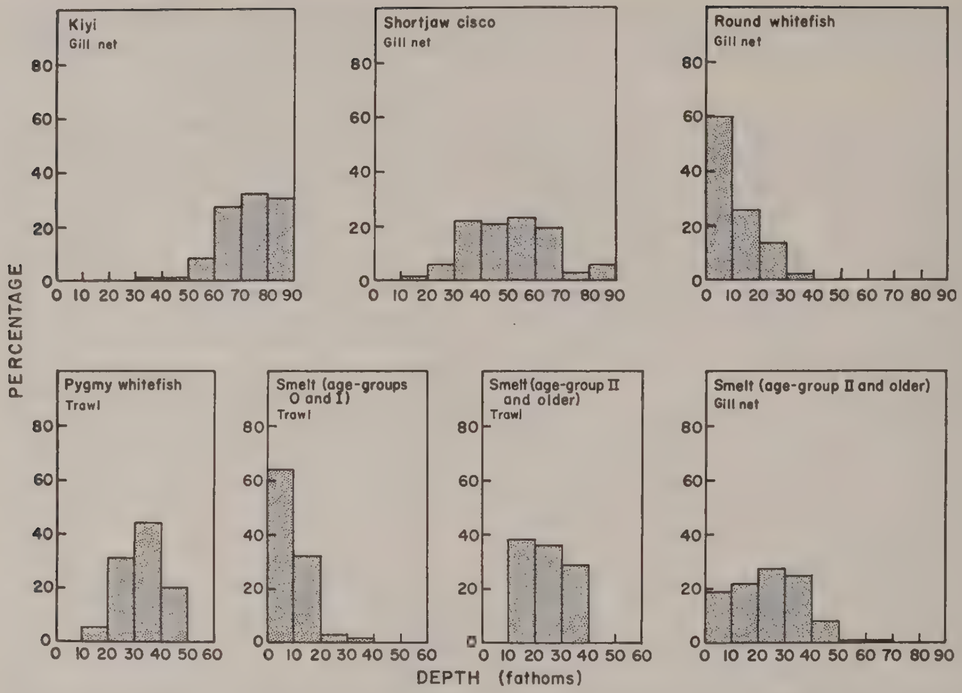

FIGURE 3.—The all-season average percentages of various species captured per 15-minute trawl tow or per 1,000 feet of gill nets lifted according to depth.

Round whitefish

Round whitefish were most abundant at < 20 fathoms and none were taken at depths greater than 39 fathoms (Figure 3). Although summer data are missing at depths shallower than 19 fathoms, there is some evidence that the round whitefish move inshore with progress of the seasons (Table 5). The catch at < 10 fathoms was slightly higher in the fall than in the spring, and the values at 10–19 fathoms decreased from spring to summer. The catches at 20–29 fathoms were extremely small in all seasons, but the abundance at this depth was lower in summer and fall than in the spring.

Koelz (1929) also suggested that the round whitefish was mainly a shallow-water species which exhibited an inshore movement during the summer and fall. The maximum depths from which he reported round whitefish were 23 fathoms in Lake Michigan and about 20 fathoms in Lake Huron.

Pygmy whitefish

The data on pygmy whitefish from trawls (Table 4) revealed no seasonal changes in depth distribution. The all-season bathymetric range of the species extended from 10 to 49 fathoms; the largest catches were at 30–39 fathoms (Figure 3).

The present findings agree well with those of Eschmeyer and Bailey (1955), who indicated that pygmy whitefish in Lake Superior lived at 10–59 fathoms but were most common at 30–34 fathoms. They observed little change in the seasonal distribution of the adults, but the abundance of I-group fish increased somewhat at depths greater than 29 fathoms as the season progressed.

Smelt

Most of the 0- and I-group smelt from trawls (Table 4) were taken at < 10 fathoms, and only an occasional fish was taken below 19 fathoms (Figure 3). The II-group and older smelt from trawls were nearly evenly distributed between 10 and 39 fathoms; they were rarely captured above 10 fathoms, and none were found below 39 fathoms. Fewer smelt were caught at all depths in the summer than in the spring and fall.

The II-group and older smelt from gill nets (Table 5) were most common at 10–39 fathoms, but their range in distribution extended from the shallowest water fished to 69 fathoms (Figure 3). The catches of smelt from gill nets in the summer declined sharply in shallow water (< 20 fathoms) and increased in deeper water (20–49 fathoms). The fish returned to shallow water in the fall.

Although the seasonal records for gill nets suggest that II-group and older smelt move offshore in the summer and return to shallower water in the fall, additional evidence is available that smelt move off the bottom during the summer. Scanning with a sensitive depth recorder aboard the R/V *Siscowet* during the early summer of 1961 revealed concentrations of fish 8 fathoms below the surface, in water 22 fathoms deep. A midwater trawl towed through this concentration caught 121 smelt of all sizes.

A discrepancy exists between the data from the two gears. Nearly all of the II-group and older smelt from trawls were taken at 10–39 fathoms, whereas gill nets took sizable numbers at < 10 fathoms and a few were taken at depths to 69 fathoms. These differences are unexplained.

Dryer et al. (1965) indicated that smelt were rare in stomachs of lake trout captured in Lake Superior at depths greater than 35 fathoms. Among lake trout collected in shallower water, smelt were an important food only during February through June.

Longnose sucker

Longnose suckers were most abundant at < 20 fathoms in all seasons (Table 5); with the exception of one fish taken at 50–59 fathoms, no longnose suckers were taken below 39 fathoms (Figure 4). The catches at 10–29 fathoms suggest that the fish move offshore in the fall. The smaller catches at various depths in spring and early summer may reflect a temporary stream residence for spawning.

Burbot

Although burbot were taken at several depths in all seasons, the catches gave no evidence of seasonal changes in distribution. The all-season averages (Table 5, Figure 4) show a wide distribution from the shallowest water to 69 fathoms. The largest catches were at 10–19 fathoms.

The present data agree well with those from Lake Michigan where Van Oosten et al. (1946) found no evidence of seasonal movements for burbot and the all-season average catches were greatest at 10–12 fathoms.

Ninespine stickleback

The ninespine stickleback was the most common fish in trawl catches from the Apostle Islands region (nearly 30,000 were taken in 1958–63). The wide variation in individual catches of sticklebacks from all depths and seasons makes difficult the detection of possible seasonal differences. Catches often varied from less than 10 to over 1,000 individuals in consecutive tows at the same depths and locations. Variation in the catches may have been caused by schooling. Because of the excessive variability of individual catches, averages based on even a large number of tows may not be dependable.

Ninespine sticklebacks were taken in trawls at all depths to 59 fathoms (Table 4, Figure 4). The fish were very abundant at < 10 fathoms and at 50–59 fathoms. Ninespine sticklebacks were found in the stomachs of lake trout (Dryer et al., 1965) caught at less than 36 fathoms in April–June and at nearly all depths in July–December.

Trout-perch

The number of trout-perch also varied widely and erratically in trawl catches from the Apostle Islands region. The fish exhibited no seasonal trends in distribution. The all-season averages indicate that trout-perch were widely distributed down to 49 fathoms (Table 4, Figure 4) and that they were most abundant at 10–19 and 30–39 fathoms. No

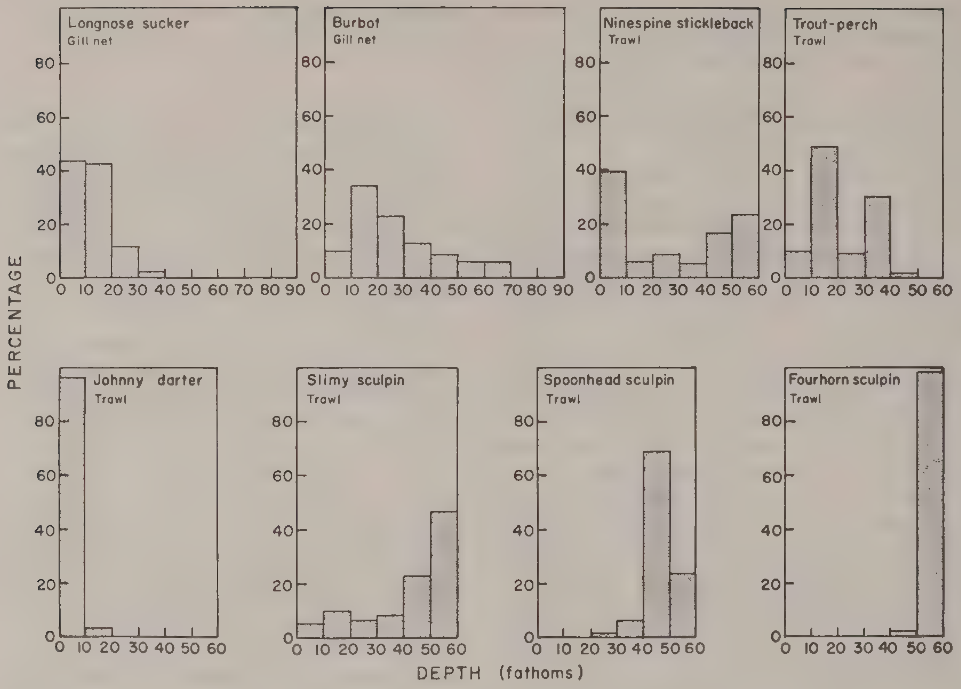

FIGURE 4.—The all-season average percentages of various species captured per 15-minute trawl tow or per 1,000 feet of gill nets lifted according to depth.

trout-perch were captured at depths greater than 49 fathoms.

Johnny darter

Of the relatively few johnny darters taken in trawls (Table 4), nearly all (96%) were from < 10 fathoms (Figure 4). Johnny darters were not caught below 19 fathoms.

Slimy sculpin

The slimy sculpin was caught at all depths but tended to be more abundant in deeper water. Largest catches were at 50–59 fathoms (Table 4, Figure 4). No evidence of seasonal changes in distribution could be detected. The abundance of the slimy sculpin in the Apostle Islands region varied somewhat according to geographical location; consequently, the fluctuations in catches from the same depths at different locations may have obscured the true bathymetric distribution. Despite irregularities in the data, the fish appeared to be most common at depths greater than 40 fathoms.

Dryer et al. (1956) found Cottidae (mostly slimy sculpins) far more common in stomachs of lake trout caught below 35 fathoms than in stomachs of fish from shallower water. Deason (1939), who studied the distribution of Cottidae in Lake Michigan from their occurrence in stomachs of lake trout and burbot, stated that the shallowest depth of capture of lake trout and burbot whose stomachs contained slimy sculpin was 13.5 fathoms and the maximum was 70 fathoms.

Spoonhead sculpin

The spoonhead sculpin was more restricted to deeper water than the slimy sculpin. No fish were taken shallower than 20 fathoms and abundance increased with depth to 40–49 fathoms (Table 4, Figure 4). The numbers captured in trawls were insufficient to demonstrate seasonal differences in distribution.

The spoonhead sculpin was taken in minnow seines from 2 fathoms in Lake Michigan and was found in stomachs of lake trout and burbot captured at 13.5 to 73 fathoms (Deason, 1939).

Fourhorn sculpin

The fourhorn sculpin (also known as deepwater sculpin) inhabited only the deepest water fished with trawls in the Apostle Islands region. The average catch per tow increased from 0.5 at 40–49 fathoms (none taken in shallower water) to 35.0 at 50–59 fathoms (Table 4, Figure 4). The capture of small numbers of fourhorn sculpins in 1-inch-mesh gill nets fished at 85 fathoms by the R/V *Siscowet* proved that the species inhabits depths far greater than were fished by trawls in the present study. The R/V *Cisco* captured fourhorn sculpins in trawls fished at 200 fathoms in Lake Superior in 1953.[3]

The distribution of fourhorn sculpins in Lake Michigan appears to range from approximately 25 to 100 fathoms (Deason, 1939). They were most common in stomachs of lake trout and burbot captured at 40–75 fathoms.

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Cycling of Trace Elements in the Estuarine Environment. I. Movement and Distribution of Zinc 65 and Stable Zinc in Experimental Ponds

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ABSTRACT: Observations were made on the movement and distribution of zinc 65 and the distribution of stable zinc in water, sediments, and macrobiota of two estuarine ponds. Pond I was essentially a closed system and Pond II was connected to an adjoining estuary. In Pond I, zinc 65 moved rapidly from the water to other components of the ecosystem so that after 1 day only 66% of zinc 65 remained in the water. In Pond II, approximately 82% of zinc 65 was flushed out within 1 day by tidal exchange of water between the pond and the adjoining estuary; of the zinc 65 remaining, 36% was in bottom sediment, 59% in the water (one-third of the amount in the water was associated with suspended material), and 5% in the macrobiota. After 100 days, the bulk of zinc 65 and stable zinc was in the sediment of each pond. Analysis of specific activity ($\mu\mu$c zinc 65/μg zinc) in components of the ecosystem indicated that the exchange of zinc between sediment and water dominated the cycling of this element and controlled the distribution of zinc 65 in the ponds.

Introduction

Trace elements are cycled continuously through water, sediments, and biota of estuarine environments. Chemical composition of the water helps determine the physical-chemical states of the elements and their availability to sediments and organisms. Sediments concentrate many trace elements from sea water by sorption phenomena which include physical and chemical processes. In shallow bodies of water, such as estuaries, the rates of exchange of elements between sediments and water may control the availability of elements to the biota. At least three mechanisms exist by which trace elements can become associated with estuarine biota: absorption through membranes; accumulation of particulate material; and adsorption at cell-water interfaces. Zinc, one of the trace elements, is relatively abundant in several species of marine organisms and is essential for their growth and reproduction.

Zinc occurs in all three phases of the estuarine environment—water, sediments, and biota. Zinc has been postulated to occur in sea water as $ZnCl^+$, and as Zn^{++} (Krauskopf 1956). According to Goldberg and Arrhenius (1958) approximately 10% of the total amount of the zinc is present as sulfates. Rona et al. (1962) showed that a portion of zinc in sea water exists as a non-dialyzable fraction that is ultrafilterable. This characteristic indicates the existence of a complexed form of zinc, probably organic, in sea water. Zinc also was reported to occur in the ionic state in sea water (Waldichuk 1961) and in the ionic-

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particulate state (Mauchline and Templeton 1964). In the sediment phase zinc may occupy spaces in the lattice structure of clays (Elgabaly and Jenny 1943) or may be sorbed onto surfaces or interfaces. In the biotic phase this element may be sorbed onto surfaces or may be specifically bound to enzymes such as carbonic anhydrase and alcohol dehydrogenase (Hoch and Vallee 1958). Because zinc occurs in trace quantities, zinc 65, a radioisotope of zinc, is especially useful in delineating the cycling of zinc in estuarine environment.

Radioactive isotopes have been shown to be effective in following the movement of elements in aquatic environments. For instance, phosphorus 32 has been used in several studies on the kinetics of phosphorus exchange and the distribution of this element in ponds, lakes, and streams (Hutchinson and Bowen 1947, Hayes et al. 1952, Rigler 1956, Ball and Hooper 1963, Whittaker 1961). Also, phosphorus 32 has been used to study exchange of phosphorus between estuarine water and sediments (Pomeroy 1965). Radioactive sodium has been used to follow the movement of sodium in a chemically stratified lake (Likens and Hasler 1960) and in an ice-covered lake (Likens and Hasler 1962). Absorption of cesium 137 by an aquatic community has been studied by Pendelton (1958). The movement of zinc 65 which entered the lagoon of Rongelap Atoll from air-borne fallout was investigated in detail by Joyner (1962), who also studied effects of biological specificity of zinc on the distribution of zinc 65.

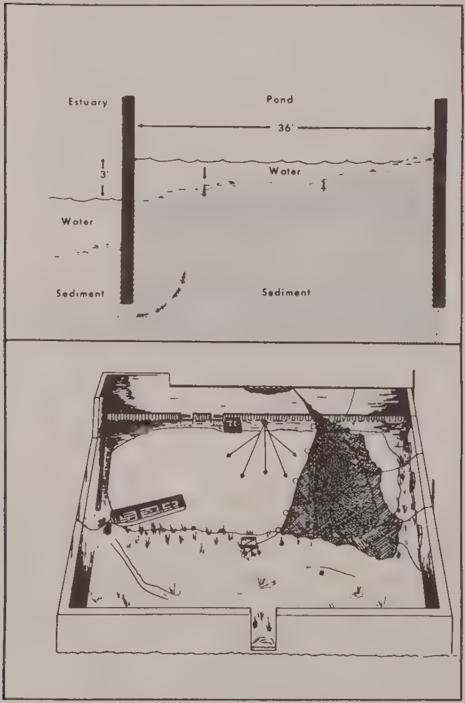

Fig. 1. Diagrammatic sketches of experimental ponds. Arrows in Pond I (upper) indicate flow of water and in Pond II indicate location of pipe through which water was exchanged with adjoining estuary. The position of the sampling net is shown in Pond II.

The purpose of our research was to follow the movement of zinc 65 in the water, biota (macrobiota), and sediment of two experimental ecosystems, to determine some of the factors which control this movement, and to determine if the distribution of zinc 65 is related to the distribution of stable zinc in the system.

Experimental Procedure

Two concrete-walled ponds which adjoined a portion of the estuary surrounding Pivers Island, N. C., were modified and used as experimental environments. When one of the ponds (Pond I) was filled with 45 m^3 of sea water from the estuary, the level of water in the pond was higher than the mean tidal level in the estuary (Fig. 1). As a result, water pumped into the pond seeped through sediments into the estuary. To increase the retention time of water, the pond was drained, a layer of sediment about 6 cm thick was removed, and a plastic sheet (4 mil thick) was stretched over the bottom and covered the sides of the pond. The layer of sediment was then placed on the plastic sheet. Approximately 168 m^2 of sediment was covered with water. An inflow of sea water (9,600 l/day) from the estuary was maintained to balance seepage that occurred around the edges of the plastic. The other pond (Pond II), in which the bottom was undisturbed, was connected to the adjoining estuary through a tile pipe, 8 inches in diameter (Fig. 1). The end of the pipe in the pond was covered with ¼-inch-mesh net to prevent entry or exit of the larger organisms. The pond contained 78 m^3 of water at low tide and 173 m^3 at high tide. Approximately 186 m^2 of sediment was covered with water at high tide. The distribution of sediment particles by size to a depth of 6 cm in Pond I was 93% sand (>0.05 mm), 1% coarser silt (0.05–0.025 mm), 1% coarse silt (0.025–0.005 mm), 0.5% fine silt (0.005–0.002 mm), and 3.5% total clay (<0.002 mm). In Pond II the distribution was 79% sand, 12% coarser silt, 3% coarse silt, 1% fine silt, and 4% total clay.

Organisms were collected in the Beaufort, N. C., area and placed in the ponds for 1 week before the zinc 65 was added to the water. Flora in Pond I included 150 marsh grass plants (*Spartina alterniflora*)—and 4 seaweeds (*Enteromorpha* sp., *Rhizoclonium tortuosum*, *Ectocarpus* sp., and *Agardhiella tenera*) that entered the pond from the estuary. Invertebrate fauna in the pond included 20 American oysters (*Crassostrea virginica*), 20 hard clams (*Mercenaria mercenaria*), 10 blue crabs (*Callinectes sapidus*), 10 mud crabs (*Panopeus herbstii*), and 20 snails (*Littorina irrorata*). Two species of marine vertebrates were included—40 Atlantic croakers (*Micropogon undulatus*) and 20 mummichogs (*Fundulus heteroclitus*). A similar community was placed in Pond II with the following exceptions: seaweeds were not trapped in the pond; there were approximately 10,000 indigenous plants of marsh grass; and 20 scallops (*Aequipecten irradians*) and 15 blue crabs, comprised part of the community.

Ten millicuries of zinc 65 (specific activity = 0.43 c/g) in the form of ionic zinc in 0.92 N HCl was added to Pond I on June 9, 1963, by siphoning a solution of the radioisotope into a stream of water and spraying the stream over the surface of the pond. At this time, the salinity of the water was 28.2‰, the temperature 29.6°C, and the pH 8.4. During the experiment the salinity ranged from 22.0 to 36.1‰, the temperature from 23.8 to 32.4°C, and the pH from 7.4 to 9.0. An equal amount of zinc 65 with the same specific activity was added to Pond II immediately following ebb tide on April 13, 1964. The salinity of the water at this time was 26.6‰ and ranged from 24.9 to 34.8‰ during the experiment; the temperature ranged from 17.0 to 29.0°C; the pH was 7.9 and ranged from 7.7 to 8.2. At the time the zinc 65 was introduced into Pond II, there were 40 mg (wet wt) of suspended material per liter of water.

Samples of water, biota, and sediment were removed from the ponds periodically and analyzed for zinc 65. Water samples were taken from the middle of the ponds in 900-ml sampling jars. The animals in Pond I, with the exception of the blue crabs, were maintained in cages, whereas those in Pond II swam freely and were sampled by trapping them in a large net (Fig. 1). Separate measurements of radioactivity were made on three plants of marsh grass at each sampling. Sediment cores were taken from the middle and four corners of the pond with a lucite sampler (designed by Dr. R. B. Williams), 5 cm in diameter, that penetrated 18 cm into the sediment. These samples were separated into 2-cm sections for analysis. In order to express the radioactivity content of the sample as specific activity (ratio of zinc 65 to total zinc), three individuals of each species, three samples of the water, and a composite sample of sediment were removed after 100 days and analyzed for total zinc content.

The zinc 65 content of the components from the ponds was measured with a single-channel spectrometer and a liquid scintillation detector (11 cm in diameter x 22 cm in length), which was large enough to hold live animals. Measurements were corrected for decay, machine efficiency, geometry, and background radioactivity. We detected 0.002 μc of zinc 65 per liter of water at the 95% confidence level. When the zinc 65 content of the water was below this concentration it was recorded as 0. For analysis, organisms (except fish) were wrapped in a thin plastic sheet; fish were placed in dark glass bottles filled with sea water containing no zinc 65; and sediments were inserted into 100-ml plastic cups. Fish were analyzed for zinc 65 for 3 min. and other samples were analyzed for 10 min. or until 10,000 counts were obtained. Unless otherwise specified, 10 individuals were analyzed separately and the average value for the 10 is reported.

The concentration of zinc in the various samples was determined by using a dithizone-extraction technique after preliminary preparation of the samples. The following procedure is an adaptation of existing methods. Sea water was prepared for analysis of total zinc by heating 200 g of sea water with 10 ml of concentrated HNO_3 until only sea salt remained. The residue was then redissolved in deionized water. In the determination of extractable zinc, no preliminary treatment was used for the water. Biological materials were prepared by first dissolving the sample in concentrated HNO_3. Fat and silica were removed by filtration and the remaining solution was diluted to 250 ml. Aliquots of this solution were then dry-ashed at 450°C to destroy organic matter. The residues were dissolved and neutralized with 2N HCl. Sediments were first dry-ashed at about 450° to 475°C, and then fused with Na_2CO_3. The melts were dissolved and neutralized with 6N HCl, and the solution made up to 100 ml. After the sample was prepared, it (or an aliquot) was transferred to a separatory funnel and made up to 200 ml with deionized water. Two ml of tartrate solution, 50 ml of buffer-complexer solution, and 10 ml of 0.002% dithizone in CCl_4 were added and the solution was extracted for 2 min. The complexers masked any interfering elements (see Gettler and Bastian 1947, and Vallee and Gibson 1948), and the dithizone extracted 94 ± 2% of the zinc into the CCl_4 phase. The absorbance of the CCl_4 phase was determined at 530 mμ and the concentration of zinc computed from comparison with the absorbance of a standard solution. Blanks were carried through the entire procedure.

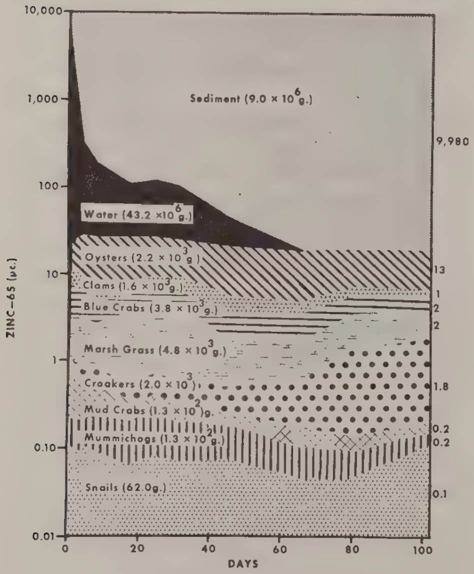

Fig. 2. Distribution of zinc 65 in Pond I with time. A total of 10,000 μc is in the pond at any specific time. (The amount of zinc 65 (μc) in each component after 100 days is shown at right margin.)

The accuracy and precision of the sea water analysis were determined by adding known quantities of ionic zinc to fifteen 200 ml samples of zinc-free sea water (salinity 24‰) and analyzing for zinc. The standard deviation was ±14% and relative error 2%.

Movement of Zinc 65 in Pond I

Zinc 65 moved rapidly from the water to the sediments and biota of the ecosystem (Fig. 2). The zinc 65 content of components in the pond was determined 1, 3, 8, 18, 66, and 100 days after the zinc 65 was added to the pond. The variation in the zinc 65 content of organisms sampled on the 1st and 66th day is shown in Table 1 and is representative of the variation found in organisms sampled at other times. Fourteen hours after the addition of the isotope, 66% of the zinc 65 had been lost from the water. This initial loss of radioactivity from the water was due probably to adsorption onto exposed surfaces in the environment, and to exchange with the stable element in other components, particularly the sediments. After 10 days, 97% of the isotope had disappeared from the water.

Sediments accumulated more zinc 65 on a total-weight basis than did the biota. Since there was no detectable loss of zinc 65 from the pond, zinc 65 content of the sediment was estimated by subtracting the amount in the water and biota from the amount of zinc 65 originally added. After 100 days the sediment contained over 99% of the zinc 65 in the pond. The zinc 65 occurred in the biota and sediment in approximately the same proportion as the stable zinc. Also, the physical arrangement of the pond caused the water containing zinc 65 to flow around a large area of highly sorptive sediment particles and no doubt contributed to the partition of the isotope between the sediments and biota.

All of the organisms analyzed contained zinc 65 (Fig. 2). Invertebrates accumulated zinc 65 rapidly, reaching maximum concentration levels within 2 to 7 days. Oysters accumulated zinc 65 at a faster rate and to higher levels than the other organisms. Mud crabs accumulated almost as much zinc 65, per unit weight, as did oysters during the first 2 days of the experiment, but after this time the zinc 65 content of the crabs fluctuated. Since this species of crab feeds on detritus, these fluctuations might be caused by the ingestion and excretion of detrital material containing zinc 65. The vertebrates in the pond did not accumulate as much zinc 65 per unit weight as the invertebrates. During the course of the experiment, some croakers and mummichogs escaped from their cages and swam freely in the pond. When recaptured, these animals had grown more and accumulated more zinc 65 than those in the cages. To eliminate this "cage effect" all organisms were allowed to swim freely in the second pond experiment.

Seaweeds that appeared in the pond after zinc 65 was no longer detectable in the water proved to be excellent indicators of the presence of the isotope, since they accumulated zinc 65. These plants may have been present as spores at the time the zinc 65 was added or they may have entered the pond later in water from the adjoining estuary. Regardless of how they entered the pond, 45 days after the mature plants appeared, *Ectocarpus* had accumulated 71 c.p.m. of zinc 65 per gram of fresh tissue, *Rhizoclonium* 42 c.p.m., *Agardhiella* 11 c.p.m., and *Enteromorpha* 8 c.p.m.

TABLE 1. A comparison of zinc 65 content of whole organisms (wet wt) in experimental ponds, 1 and 66 days after introduction of isotope.

Organisms	Pond I[1]	Pond II[1]
	(1 day)	
	$\sqrt{\mu\mu c/g}$	$\sqrt{\mu\mu c/g}$
Oysters	77 ± 21 (10)	33 ± 8 (10)
Mud crabs	54 ± 32 (5)	Not sampled
Clams	39 ± 17 (9)	22 ± 6 (10)
Snails	38 ± 10 (10)	Not sampled
Marsh grass	35 ± 11 (3)	16 ± 2 (3)
Blue crabs	32 ± 4 (10)	17 ± 5 (5)
Mummichogs	26 ± 9 (10)	Not sampled
Croakers	13 ± 3 (10)	7 ± 2 (10)
Scallops	Not present	75 ± 4 (10)
	(66 days)	
Oysters	73 ± 8 (8)	31 ± 9 (10)
Mud crabs	20 ± 5 (5)	Not sampled
Clams	20 ± 6 (8)	17 ± 3 (10)
Snails	20 ± 6 (10)	11 ± 6 (5)
Marsh grass	13 ± 8 (3)	4 ± 1 (3)
Blue crabs	22 ± 1 (3)	11 ± 5 (5)
Mummichogs	18 ± 6 (3)	Not sampled
Croakers	22 ± 2 (10)	10 ± 1 (8)
Scallops	Not present	38 ± 7 (3)

[1] Zinc 65 content is given as the mean, ±1 standard deviation; number of animals in parentheses.

The rooted plant, *Spartina*, an important primary producer in many estuaries, accumulated zinc 65 rapidly for 24 days and then lost approximately half of the activity during the following 24 days. The roots of these plants contained more zinc 65 than the stalk or leaves at each sampling. Seeds produced by plants after 130 day contained about the same amount of zinc 65 as the roots.

Movement of Zinc 65 in Pond II

The partition of zinc 65 and stable zinc between the "soluble" and "particulate" phases in the water of the pond was observed periodically for 96 hours. The total amount of zinc 65 and stable zinc in a sample of water (900 ml) was measured and the sample filtered through a 0.45 μ Millipore filter. That fraction of zinc passing through the filter was designated as soluble and the remainder as particulate.

Corrections were made for zinc 65 adsorbed to the filtering apparatus. The particulate phase in the water of this pond consisted chiefly of siliceous particles and included a small amount of living matter. Apparently the concentration of zinc 65 in both phases was approaching equilibrium with the stable zinc after 24 hours, since the percentage of each in the two phases was approximately the same. The amount of particulate zinc 65 ranged from 18 to 33% of the total zinc 65 present in the water and the stable zinc in the particulate state ranged from 9 to 30%. Zinc 65 associated with the particulate matter in the water is important ecologically because the sedimentation of particles that have accumulated zinc 65 is often a mechanism for transporting this isotope to bottom sediments and to bottom-dwelling organisms.

Zinc 65 moved rapidly from the water to the sediment and biota (Fig. 3) but the exchange of sediment-sorbed zinc 65 back to the water was relatively slow. Components of the pond were analyzed for zinc 65 after 1, 7, 25, 66, and 100 days after the isotope was added to the pond. Variation of zinc 65 content of the organisms on the 1st and 66th day is shown in Table 1. After 1 day, measurements of the zinc 65 content of water, biota, and sediment showed that approximately 82% of the zinc 65 introduced into the pond was flushed out by tidal exchange. According to calculations based on flushing rates of the water in the pond, 81% of the zinc 65 should have been lost through tidal exchange in 24 hours. Of the zinc 65 remaining, 36% was in the bottom sediment, 59% in the water (one-third of the amount in the water was associated with suspended material), and 5% in the biota. After 110 days, no zinc 65 was detectable in the water; sediments contained 99.4% of the zinc in the pond and biota contained the remainder. The upper 6 cm of sediments lost 325 μc of zinc 65 in 103 days through exchange with stable zinc in the water and migration of the isotope to deeper layers.

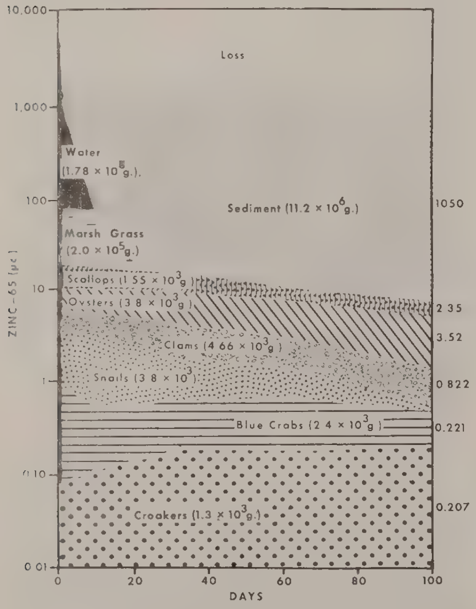

Fig. 3. Distribution of zinc 65 in Pond II with time. A total of 10,000 μc is in pond or accounted for by loss from tidal exchange at any specific time. (Amount of zinc 65 in each component after 100 days is shown at right margin.)

TABLE 2. Comparison of ratios of filtering rates and zinc 65 and stable zinc content of scallops and oysters to those of clams.

Organisms	Average[1] filtering rate	Zinc 65 content[2] after 1 day	Average[3] stable zinc content
Scallops	3.0	3.7	4.2
Oysters	2.3	1.9	8.0
Clams	1.0	1.0	1.0

[1] Scallops—Chipman and Hopkins (1954); oysters—Galtsoff (1965); clams—Rice and Smith (1958).

[2] Average values for 10 organisms of each species.

[3] Average values for 3 organisms of each species.

The filter-feeding mollusks accumulated more zinc 65 than the other organisms and after 24 hours contained 76% of all the zinc 65 in the biota. Scallops accumulated zinc 65 at a faster rate and to a higher level during the first 24 hours than did the oysters and clams. On the first day the organisms contained zinc 65 in almost direct proportion to their filtering rates, but the relation did not hold for stable zinc content (Table 2); scallops accumulated more zinc either by passing more water over their tissues than did the other organisms or by filtering more particulate matter from the water, or by both processes. A similar relationship between the accumulation of zinc 65 and filtering rates was found in the laboratory when scallops, oysters, and clams were exposed to Millipore-filtered sea water containing zinc 65 (C. L. Schelske, unpublished data). These results indicate that zinc 65 was accumulated primarily by an adsorption-exchange process during the initial phase of uptake.

Comparison of the Two Ecosystems

Organisms in Pond II contained less zinc 65 at each sampling period than those in Pond I even though the same amount of radioisotope was released in each pond. Most of this difference undoubtedly resulted from the greater dilution of the zinc 65 in Pond II. Tidal exchange contributed to this dilution and steadily lowered the concentration of zinc 65 in the water and thus reduced the amount available to the organisms. Approximately 80% of the zinc 65 introduced into Pond II was lost within 24 hours through tidal exchange of water between the pond and estuary. An amount of the isotope proportional to the amount of water exchanged was lost during each succeeding tidal cycle. In Pond I, however, there was no tidal exchange of water so theoretically all of the zinc 65 introduced into this pond was available to components of the ecosystem.

The distribution of zinc 65 between the macrobiota and sediment of the two ponds was similar to the distribution of stable zinc (Table 3) and, as mentioned previously, the specific activity of biota and sediment were similar. The values for the macrobiota reported in Table 3 were multiplied by abundance (standing crop wet weight) of each organism to obtain the distribution of zinc in the ponds. The sediment contained the bulk of zinc in the experimental ecosystems, and the distribution of zinc was similar to that found in a bay in Texas (Parker 1962). Our results, like those of Parker, indicated that the sediments serve as a reservoir for zinc in the estuarine environment. Additional information on the factors that influenced the distribution of zinc in the ecosystem can be obtained by observing the specific activity of the water, biota, and sediment.

Certain ecological trends can be detected by comparing the specific activity in selected components of the ecosystem (Fig. 4). The specific activities in sediments and organisms were based on the mean zinc concentration in each of these components determined 100 days after the experiment was initiated, compared with their mean zinc 65 content at the time of sampling. The stable zinc was not analyzed at each sampling period because this would have required that samples be removed permanently from the system and would have reduced the number of animals for measurements of radioactivity, and might have altered the ecology of the pond. To insure minimum fluctuations in zinc concentrations in the organisms, however, all components were allowed to equilibrate in each pond for 7 days before the experiment was started. The stable zinc and zinc 65 content of the water was determined at each

TABLE 3. Distribution of zinc and zinc 65 in experimental ponds, 100 days after zinc 65 was introduced.

Pond number, and phase	Fresh weight	Zinc	Zinc 65	Zinc	Zinc 65
	(g)	*(mg)*	*(μμc)*	(%)	(%)
Pond I					
Water	43.2×10^6	661	Background level	0.1	Background level
Macrobiota	14.9×10^3	846	20	0.1	0.2
Sediment (upper 6 cm)	33.0×10^6	615×10^3	9,980[1]	98.8	98.8
Pond II					
Water	79×10^6	390	Background level	1	Background level
Macrobiota	22×10^4	4,777	5	4	5
Sediment (upper 6 cm)	11×10^6	110×10^3	771	95.0	94.0

[1] Calculated.

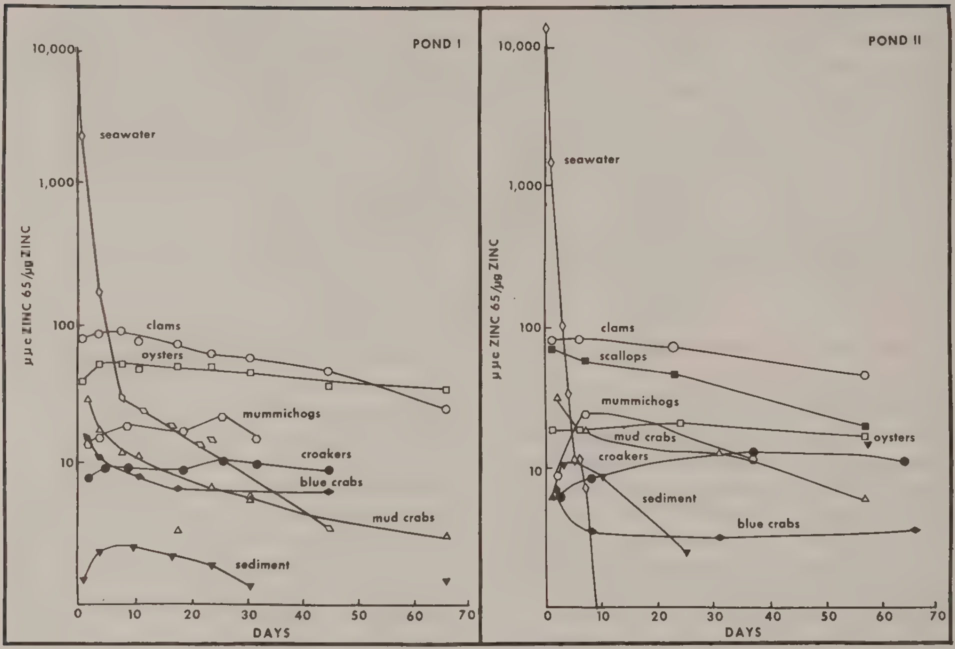

Fig. 4. Specific activity of components in experimental ponds. The specific activity of the water at the time zinc 65 was introduced into the pond ("0" days) was 18,100 μμc zinc 65/μg zinc in Pond I and 14,200 in Pond II.

sampling period. Stable zinc content of the water in Pond I (the "closed" system) ranged from 8.1 to 44 μg Zn/g water and that in Pond II from 4.9 to 9.4 μg Zn/g water.

The curves representing the variation of specific activity in organisms with time can be grouped according to shape into three types which correspond to three classes of organisms present—mollusks, crustaceans, and fish. Each of the mollusks exhibited a slightly different type of specific activity-time curve. The specific activity in the clams increased to a high value initially and then decreased gradually. Assuming that the zinc 65 and stable zinc in the water were in the same chemical form, this could be due to a rapid turnover of this element. In scallops, the specific activity increased to almost the same level as that of clams, but decreased more rapidly. Conversely, oysters had a much lower specific activity than did the clam and decreased more slowly. It appears that oysters possess at least one large, slow-moving compartment of zinc or were obtaining zinc 65 from a source other than the water. The specific activity in the crustaceans initially followed the trend of that of the water, indicating the presence of a small compartment of zinc with a rapid turnover rate, along with a much larger slowly exchanging compartment. The specific activity curves for fish showed less relationship to the water than did the crustaceans or mollusks.

The sediments in both ponds contained the greatest total amounts of zinc and zinc 65 of any of the components. The low specific activity of the sediments indicated that most of the zinc was probably bound in slowly exchangeable forms. If a large part of the zinc in the sediments had a slow turnover rate, the specific activity of the remaining portion, which was small but rapid, would be considerably higher than the value indicated by the specific activity-time curves. This is because total zinc concentrations, rather than readily exchangeable zinc concentrations, were used in computing these values. Thus, sediments containing a compartment with a rapid turnover rate, which had large amounts of zinc in relation to the biota and water, appeared to be one of the controlling factors in the cycling and distribution of zinc 65 in the experimental ponds.

Observations on the movement and distribution of zinc in the experimental ponds are comparable with those reported by other investigators. It was shown in laboratory experiments by Bachmann (1963) that oxidized sediments in 22 days removed as much as 96% of the zinc added to the water. He suggested that in natural lakes the sedimentation of particles containing zinc would result in an accumulation of this element by bottom sediments. Samples of water, phytoplankton, and sediment from the Columbia River near the Hanford Atomic Energy Reservation, Washington, contained measurable amounts of zinc 65 (Watson 1965) and, although phytoplankton concentrated zinc 65 to a higher level than sediments, the sediment contained more of this isotope on a total weight basis. Seymour and Lewis (1964) separated particulate material in Columbia River estuarine water by filtration and found that 69% of zinc 65 in the water remained in the filter paper. In a freshwater pond, zinc 65 introduced into water overlying a sand substrate became associated primarily with suspended matter rather than with bottom sediments (Brungs 1963). This association could have been the result of uptake of zinc 65 by large quantities of biotic materials in the suspended matter and relatively little uptake by the sand-size particles in the substrate. It is evident from the results of our experiments and those of other investigators that sediments are an important factor in the movement and distribution of zinc in both freshwater and marine environments.

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No. 113 — SIb

SEASONAL CYCLE OF TEMPERATURE IN THE MIDDLE ATLANTIC *

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All bathythermograph data collected during the period 1941-1961 from the Continental Shelf and adjacent slope water area between Cape Cod and Cape Hatteras has been examined and analyzed. Temperature data for 18 depth strata, and 36—10-day periods have been subjected to analysis by computer to determine the mean seasonal cycle by area, season and depth and the secular deviations during the period 1941 to 1961. A provisional heat budget has been calculated. Secular variations are related to meteorological variations and advectic processes. Biological implications of the mean temperature will de discussed.

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ARCHAEOLOGICAL POTENTIAL OF THE ATLANTIC CONTINENTAL SHELF*

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ABSTRACT

Early man lived in eastern United States 11,000 years ago when most of the now-submerged continental shelf was exposed. The shelf almost certainly was ranged by nomadic hunters and possibly by marine fish- and mollusk-eaters. As the sea level rose at the end of the latest glacial epoch, the advancing water disrupted and submerged any habitation sites.

The oldest radiocarbon dates for kitchen middens of marine refuse along the present shore appear to be younger than the oldest dates for kitchen middens of non-marine content. Older marine middens may be deeply submerged far out on the continental shelf. Greatest success in future exploration for these sites is likely in areas of the shelf which have received little or no cover of postglacial sediment and where rivers formerly crossed the shelf.

IT HAS BEEN KNOWN for many years that broad expanses of the continental shelves were exposed during glacial stages of the Pleistocene Epoch. The relative lowering of sea level was sufficient to move the shoreline of eastern North America as far seaward as 150 km. The shelf was exposed long enough for spruce forests to develop on Georges Bank off the New England coast (Emery, Wigley, and Rubin, 1965); and one can safely assume that appropriate climax vegetation occurred elsewhere as well.

At present the sea level is comparatively stable and it has been so for the past 3,000 to 4,000 years. During the previous 8,000 years sea level rose rapidly (Fig. 1), although not so rapidly that a man in his lifetime would necessarily be aware of any rise. During this period, the shore, especially along the Atlantic Coast from southern New England to Florida, had the general appearance of the barrier beaches of the Carolinas and Virginia, and the lagoons, sounds, and tidal marshes immediately behind these barrier beaches probably were similar to those of today.

Animal species living at present also lived then and left their remains in abundance. For example, many bottom samples from between 20 and 90 meters contain one or more empty shells of the common edible oyster, *Crassostrea virginica* (Gmelin), which lives mostly in the tidal zone and to depths of only a few meters in the coastal lagoons and estuaries. Radiocarbon dates of six of the shells show that the animals that were housed in them lived as long ago as 10,850 years (Merrill, Emery, and Rubin 1965). These shells presumably indicate the presence of ancient oyster beds since there is no evidence that they have been carried out to sea or moved any distance by water currents.

MARINE GEOLOGY

During late 1962 a long-term geological and biological investigation of the continental margin off eastern United States was begun by the U.S. Geological Survey, the Woods Hole Oceanographic Institution, and the U.S. Bureau of Commercial Fisheries (Emery and Schlee 1963). The more than 1800 well-distributed samples that were collected during 1963 and 1964 yield considerable information about the bottom sediments. Most of the continental shelf is floored by detrital sands (Fig. 1) that are coarser grained than are those nearer shore in depths of less than about 20 meters. This distribution pattern indicates that modern detrital sands which escape coastal lagoons and estuaries remain in the nearshore zone. Only the finest-grained modern sediments, such as silts and clays, are carried farther seaward, and they mostly by-pass the entire continental shelf to be deposited in deep water. The coarse-grained sands on the shelf are iron stained and solution pitted, as though they had lain exposed at the sediment-water interface for a long time. This sand is believed to be a shore or nearshore deposit formed when sea level rose at the end of the latest glacial stage. Topographic evidence of former lagoons and estuaries exists in the form of submerged beach ridges and filled marine canyons and channels. The sand thus is properly termed relict or inherited from depositional conditions different from those of the present.

The ages of oyster shells and peat fit reasonably well the standard curve of sea level during the past 35,000 years that is based upon radiocarbon dates from many kinds of materials and at many places in the world (Shepard 1963: 1–10). This curve accords with other kinds of data (Broecker and Orr 1958; Frye and Willman 1961; Emiliani 1964) in showing that sea

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* Contribution No. 1661 of the Woods Hole Oceanographic Institution.

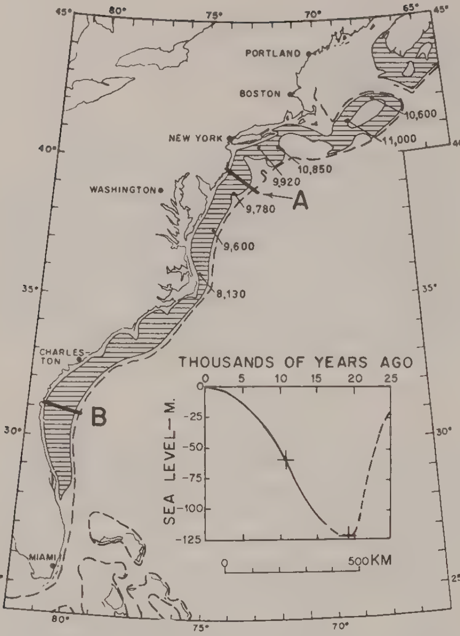

FIG. 1. Map of Atlantic Coast of the United States containing data pertinent to the possible inhabitation of the continental shelf by early man. Dashed line indicates position of seaward edge of continental shelf; lined area depicts the distribution of relict sand on the shelf; numbers are the radiocarbon ages of sub-fossil oyster shells in the area of relict sand (except 11,000, which is the radiocarbon age of an intertidal peat). The insert shows a generalized curve (relative to present sea level) of sea level during the past 25,000 years; the curve shows that about 11,000 years ago sea level was about 60 meters below the present level and most of the continental shelf was exposed. The part of the curve that is prior to 16,000 years ago is dashed owing to paucity of data points.

level rose from a low position about 19,000 years ago when continental glaciers began to melt and retreat. The level at this time was about 123 meters below the present one (Donn, Farrand, and Ewing 1962); thus the shoreline probably lay slightly seaward of the present shelf edge, which ranges from 80 meters depth at the south to 140 meters at the north of Fig. 1. Although the shoreline may have undergone several minor retreats, it eventually advanced across the entire width of the continental shelf. During the latest 5,000 years and especially during the latest 3,000 years the rate of sea-level rise, and thus of shoreline advance, markedly slowed as though a temporary equilibrium condition were being approached (Redfield and Rubin 1962; Scholl 1964).

ARCHAEOLOGY

As discussed by Haynes (1964), radiocarbon-dated sites having Clovis projectile points indicate that this culture entered northwestern United States about 12,000 years ago and spread throughout southern North America in only about 700 years. This migration appears to have been approximately contemporaneous with an abrupt warming of worldwide climate, as indicated by changes in deep-sea sediments (Broecker, Ewing and Heezen 1960). Fluted points have been found at a great many places on land in the area of Fig. 1, but radiocarbon dating appears to have been attempted at only three sites and even these results are considered indefinite (Haynes 1964). It seems certain, however, that the fluted projectile point cultures occupied the Atlantic coastal region during the period between 12,000 and 10,000 years ago (Mason 1962) when most of the present continental shelf was still exposed. That such big game as they may have sought (see remarks by Griffin 1964: 224) lived on the presently submerged area is indicated by the occasional finding of mastodon and mammoth bones and teeth by fishermen (Uchupi 1964).

Cultures represented by fluted points and associated tools (as for example Clovis and Folsom) appear to have been nomadic hunting economies (Willey and Phillips 1958). It is presumed that horn and bone were utilized for various purposes, but, like any shelters that these people may have built, there is little hope that these materials persisted on land. The advancing seas would certainly disperse any meager remnants of shelters and other devices of temporary nomadic habitations, but some of the tools may remain in marine sediments.

Archaic stage cultures (in the sense of Willey and Phillips) were developing rapidly at a time (5,000 to 6,000 years ago) when the shoreline was still well out on the present continental shelf. Such cultures were relatively sedentary and eventually produced a variety of relatively indestructible artifacts such as stone bowls and impressive evidences of long-term habitation such as large fresh water and marine shell middens that still exist in the southeast. Stone artifacts of all descriptions abound in some archaic sites, leading one to suppose similar conditions may exist on the continental shelf. This may be a vain hope, however, because great concentrations of artifacts are usually associated with a source of raw material; none of the bottom

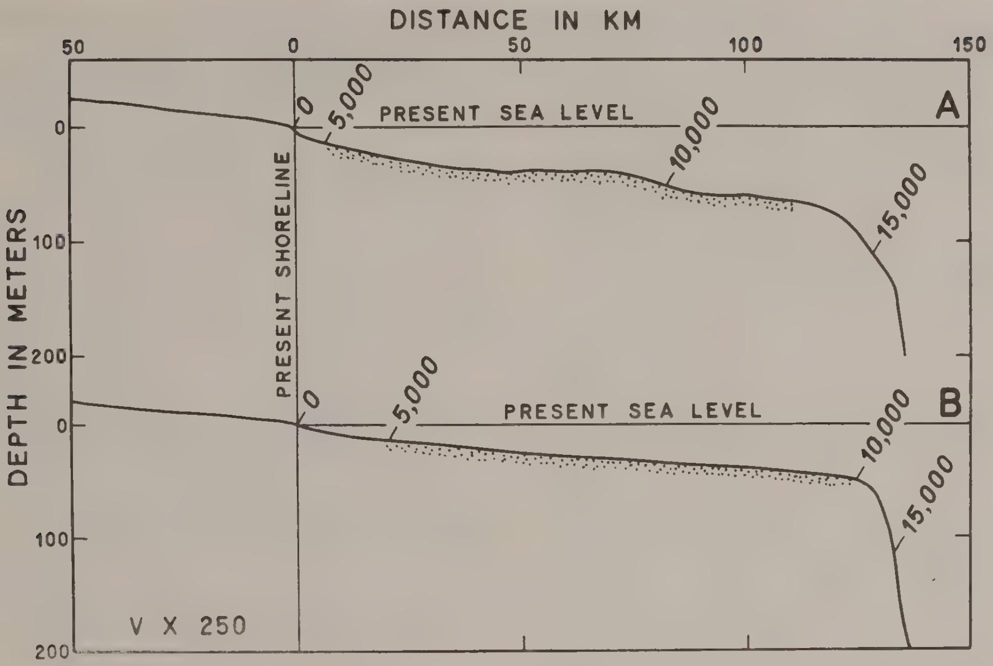

FIG. 2. Cross-sections of continental shelf at positions indicated on Fig. 1. The slant numbers represent the positions of the shoreline during the past 15,000 years; the dotted pattern denotes the part of the shelf that is underlain by relict sediments.

sampling or continuous seismic profiling done so far across the shelf indicates exposure of appropriate raw materials. Underlying the sandy sediments on most of the shelf are comparatively soft and poorly cemented marls and sandstones.

Archaic and possibly even some lithic cultures utilized both marine and fresh water mollusks. Marine shells from kitchen middens on the Pacific Coast have yielded shells having radiocarbon ages as great as 7,000 to 9,000 years (J. R. Moriarty, personal communication). To our knowledge, the oldest dated marine shell midden on the Atlantic Coast is on Sapelo Island, Georgia. This midden contains the earliest pottery and is about 3,800 years old (Griffin 1952). Preceramic fresh water shell middens occur in several states, notably on the Tennessee River in northern Alabama, and the Green River in Kentucky. The Kentucky sites may be as old as 7,000 years (Griffin 1952).

It is not surprising that older marine shell middens have not been reported on the Atlantic Coast. Assuming that such middens would be established only within a reasonable distance of the shoreline, any that were much older than 4,000 years would now be covered with at least several meters of water (Fig. 2) if not also dispersed by the advancing sea. The older ages of shells found by Moriarty are not necessarily anomalous; the shelf on the Pacific Coast is generally narrow, and it is not inconceivable that the mollusk harvest was transported a short distance to a suitable living site. The shelf off the Atlantic Coast is relatively wide, and the harvest would have to be transported great distances if 11,000 year-old shells were to be found in shell middens presently above sea level. Accordingly, one may suggest that generally the ages of marine shells in middens above present sea level should have ages inversely proportional to the width of the adjacent continental shelf. If men of the paleo-Indian period lived upon oysters and fish and inhabited the shores of the ocean or of lagoons and estuaries, the sites of their habitations are now submerged beneath the waters of the continental shelf in depths of 50 to 60 meters.

An absence of marine shells in some middens of the Atlantic Coast, particularly at their lowest levels, has been attributed by Byers (1959) and others to failure of the local inhabitants to learn to eat marine mollusks. We can hardly assume that edible marine mollusks were not available, although variations in the kinds of shells in different layers of middens of the Maine coast may reflect temporary changes in the coastal fauna resulting from variations in water temperature (R. L. Dow, personal communication).

Presently submerged habitations and structures built by early man in North America are known, but all are close to the present shoreline and are of relatively recent date. Examples are from southern California and adjacent parts of Mexico where at least six village sites are marked by numerous stone bowls and tools (Marshall and Moriarty 1964) at 0 to 12 meters in depth. Radiocarbon dating of associated lagoonal peat at one site indicates that the artifacts cannot be older than about 4,000 years (Moriarty, in press). Another site is the 4,600-year-old fish weir found during building excavations at Boston (Kaye and Barghoorn 1964). More recent sites are illustrated by burials and habitations whose bases are below water level in present salt marshes (Goggin 1948).

As pointed out by Shepard (1964), there probably exist many other sites as old as 6,000 years in the shallow waters of the coast which are accessible to divers using air tanks. Warren and Bullen (1965) have recently reported projectile points and other tools found in fill dredged from Terra Ceia Bay, Florida. Some of the points belong to the Dalton period (about 9,000 years old) and represent the first find, to our knowledge, of early archaic material offshore. Unfortunately, there apparently is no knowledge of the exact spot in the bay from which the materials of the fill were dredged.

CONCLUSIONS

Future exploration of the continental shelf by manned vehicles, particularly in the area of relict sand off the Atlantic Coast, should have a very good chance of discovering submerged evidence of habitation by man dating from earlier than 10,000 years ago. Once the difficulty of penetrating and moving about in the water environment down to about 150 meters depth is economically overcome, archaeological exploration of the sea floor may possess advantages over explorations on land, owing to lack of overburden. This advantage, however, may be partly offset by the scattering of materials produced by the passage of the surf zone over the sites.

The most promising places on the continental shelf to search for artifacts and kitchen middens must be the area of relict sand (Fig. 1) adjacent to the courses of former rivers, because of the absence of subsequent sediments. Just north of Miami the sediments consist largely of shell debris that is continuously deposited and thus may have buried possible sites. The self southeast of New York has been buried by recent clayey silts. Most of the Gulf of Maine (off Boston and Portland, Fig. 1) is too deep to have been exposed 11,000 years ago, and much of the shallower part has received a blanket of postglacial silty clays, or it is covered with ice-rafted cobbles and residual concentrations of glacial till that greatly dilute any possible stone artifacts. The shallow central area of Georges Bank (300 to 400 km. east of Boston) is also unfavorable, owing to great postglacial shifting of sand waves. There remains an area of about 250,000 square kilometers off the Middle Atlantic States that is most favorable for the search for submerged habitation sites of early man.

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Effects of Acute Gamma Irradiation on the Blood Constituents of Pinfish, *Lagodon rhomboides*[1]

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ABSTRACT: Adult pinfish, *Lagodon rhomboides,* were irradiated with a dose of either 2,000 or 5,000 R of gamma radiation. Changes in cellular blood components were followed for 34 days in fish receiving 2,000 R and for the 7 days that fish receiving 5,000 R survived. Neither radiation dose had much effect on erythrocyte numbers, hematocrit values, or hemoglobin levels. The number of thrombocytes in both irradiated groups decreased for 1 week and then slowly recovered in fish that received 2,000 R. Leucocytosis occurred 6 hours after irradiation, followed by leucopenia, which was maximal on the 3rd day. In fish irradiated with 2,000 R, leucocytes began to increase after the 3rd day, reached a maximum on the 21st day, and decreased to a low level. Leucocytosis in the pinfish receiving 5,000 R was caused predominantly by granulocytes but in fish receiving 2,000 R granulocytes and nongranulocytes contributed equally. A temporary recovery of leucocytes on the 21st day was due primarily to nongranulocytes.

Hematological responses of pinfish, *Lagodon rhomboides,* were observed following acute doses of gamma radiation. Prior investigations on the hematological response of fish to irradiation have been devoted almost entirely to freshwater species—the goldfish, *Carassius auratus* (Watson, Shechmeister, and Jackson, 1963), and the tench, *Tinca vulgaris* (Sletten, Lockner, and Hevesy, 1964). Changes in leucocyte and thrombocyte numbers in the goldfish were observed following X-irradiation; alterations of erythrocyte numbers, hemoglobin levels, hematocrit values, and leucocyte numbers in the tench were followed after cobalt-60 irradiation.

The purpose of this investigation was to determine the relative radiation sensitivities of the various cellular constituents of the blood of a marine fish and to compare some of the hematological responses of a marine fish with those of a freshwater fish.

Materials and Methods

Mature pinfish were acclimated to laboratory conditions for at least 1 week, then irradiated with 2,000 or 5,000 R of gamma radiation from a 1,500-curie cobalt-60 irradiator which delivered 26,000 ± 10% R/hr. Other fish used as controls were handled the same as the irradiated fish. The radiation doses of 5,000 and 2,000 R were chosen to study the hematological response to both a lethal and sublethal radiation dose (White and Angelovic, 1966). Following irradiation, all fish were maintained in tanks of running sea water at 23–27 C and 23–32‰ salinity.

Fish blood was sampled at 1, 6, 12, and 24 hr, and on alternate days for 34 days, except in the experiment where fish were irradiated with 5,000 R and died within 7 days. Fish were kept in the dark under constant aeration for at least 2 hours before they were anesthetized. Then the anesthetic MS-222 was added with minimal disturbance to the fish. Blood samples were obtained by severing the tail at the caudal peduncle and collecting the blood in 5-ml beakers coated

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TABLE 1. Comparison of means and ranges of blood values from unirradiated pinfish.

Year	Hemoglobin level gms %	Hematocrit value vol %	Erythrocytes $10^6/mm^3$	Leucocytes $10^3/mm^3$	Thrombocytes $10^4/mm^3$
1964	9.9	37.7	3.94	7.25	7.3
	8.5–11.2	33.0–42.0	3.29–4.96	2.5–12.5	3–9
1965	10.3	34.6	3.30	7.93	7.9
	7.8–11.7	24.5–47.0	2.40–4.14	5.0–15.5	4.5–11.5

with dried heparin. The results obtained with this procedure were reproducible.

Techniques for processing the fish blood were all modified clinical laboratory procedures. The erythrocyte, leucocyte, and thrombocyte counts, hematocrit values, and hemoglobin levels were determined by the methods of Engel and Davis (1964). Differential leucocyte counts were made on blood films which were air dried on glass slides, fixed in 100% methanol, and stained with Hemal stain. Only two types of leucocytes were classified—granulated and nongranulated. Classifications were limited to these two because of the lack of descriptive information on leucocyte cell morphology in marine fish and also because staining characteristics were often altered following irradiation with 5,000 R. The granulocytic cells were almost all acidiphilic but the nongranulocytic cells included many cellular species.

Means of determinations from 55 unirradiated pinfish taken during two successive summers were used as the control values. Fish collected in successive years showed no differences in the measured indices (Table 1).

Results

EFFECTS ON ERYTHROCYTE NUMBERS, HEMATOCRIT VALUES, AND HEMOGLOBIN VALUES

Numbers of erythrocytes were affected only slightly by radiation (Fig. 1). Counts of erythrocytes in fish receiving 5,000 R were slightly lower than in the controls for the first 5 days after irradiation but returned to the control level by the 7th day. Fish irradiated with 2,000 R had the same numbers of erythrocytes as the controls through the 19th day, but fell below the level of the controls by the 21st day, and then returned to almost the level of the control fish by the 34th day.

Hematocrits in irradiated pinfish differed only slightly from the control values (Fig. 1). From the 1st through the 7th day after irradiation with 5,000 R the hematocrits of irradiated fish fluctuated about the mean of the control values. Hematocrits from fish irradiated with 2,000 R were higher than the controls during the first 3 days, and then decreased slowly throughout the remainder of the experiment. Irradiated fish had lower hematocrits than the controls on the 34th day.

Hemoglobin levels in fish irradiated with 2,000 R changed similarly to the erythro-

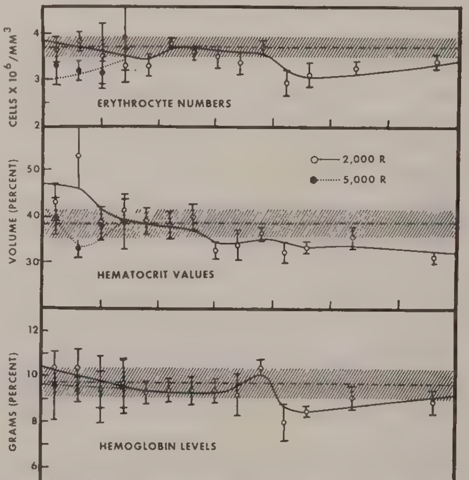

Fig. 1. Comparison of erythrocyte numbers, hematocrit values, and hemoglobin levels in the blood of irradiated and unirradiated pinfish. [The horizontal dashed line represents the mean value for all of the unirradiated fish, and the shaded area is two standard errors on either side of the mean. Solid vertical lines represent one standard error either side of the mean for five irradiated fish.]

cyte numbers; hemoglobin levels in fish irradiated with 5,000 R changed little from the 1st to 7th day, when the fish died (Fig. 1). The same general pattern appeared in the hemoglobin levels of fish which received 2,000 R. Their hemoglobin levels remained at the control value for the first 3 weeks, then decreased slightly and remained nearly constant for the remainder of the experiment.

The effects of 5,000 and 2,000 R on the erythrocyte numbers, hematocrit values, and hemoglobin levels in pinfish differed sharply from the response in the freshwater tench (Sletten, Lockner, and Hevesy, 1964). A radiation dose of 1,500 rads caused a 90% reduction in erythrocyte numbers, hematocrit values, and hemoglobin levels in the tench, but higher radiation doses produced only slight decreases in these measurements in the pinfish.

EFFECTS ON THROMBOCYTE NUMBERS

Thrombocyte numbers in both groups of irradiated pinfish decreased rapidly during the 1st week (Fig. 2). By the end of the 1st week, thrombocytes had practically disappeared in fish that received 5,000 R (Fig. 2). During the same period the thrombocytes in pinfish irradiated with 2,000 R also decreased to their lowest level. After 7 days, thrombocyte counts in these fish increased, although fluctuations were wide, and by the end of the experiment they had returned to the control level. Changes were different in goldfish blood, where 1,000 R of X-rays caused a steady decrease in thrombocyte numbers for 60 days after irradiation (Watson, Shechmeister, and Jackson, 1963).

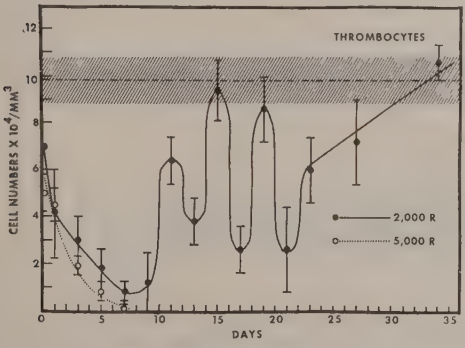

Fig. 2. Comparison of thrombocyte numbers in the blood of irradiated and unirradiated pinfish. Also see caption of Fig. 1.

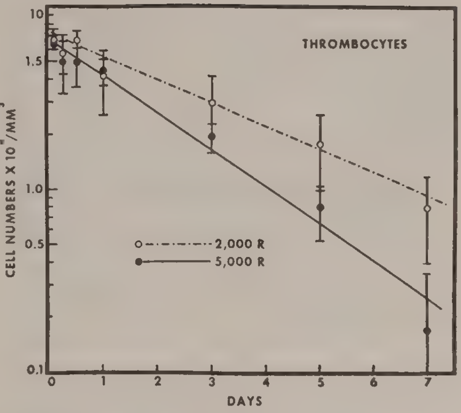

Fig. 3. Comparison of the rates of decrease in thrombocyte numbers in the blood of irradiated pinfish during the first week after irradiation. Also see caption of Fig. 1.

A comparison of thrombocyte numbers in the blood of pinfish irradiated with 5,000 and 2,000 R during the first 7 days following irradiation showed a difference in the rates of decrease in thrombocyte numbers (Fig. 3). The decrease was more rapid in the blood of the fish which received 5,000 R than in fish irradiated with 2,000 R; the rate of decrease of thrombocyte numbers appears to be dose-dependent.

EFFECTS ON LEUCOCYTE NUMBERS

Leucocyte numbers in irradiated pinfish changed during the first 24 hours at both dose levels (Fig. 4). Leucocyte numbers increased in fish which received 5,000 R, reached a maximum 6 hours after irradiation, then decreased through the 3rd day, and remained at a low level until the fish died. Fish irradiated with 2,000 R also showed increased leucocyte numbers during the first 24 hours but the increase was less than in the fish irradiated with 5,000 R. Leucocyte counts then decreased and reached their lowest level on the 3rd day after irradiation. From the 3rd through the 21st day leucocytes increased steadily until

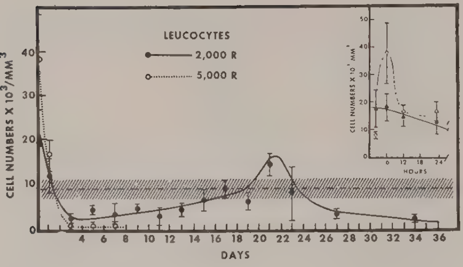

Fig. 4. Comparison of leucocyte numbers in the blood of irradiated and unirradiated pinfish. Also see caption of Fig. 1.

they were above the control level on the 21st day. This high value was apparently an overcompensation since they subsequently decreased.

A comparison of the changes in the numbers of leucocytes in the blood of fish that received 2,000 R and those that received 5,000 R, suggests that leucocyte sensitivity may be dose-dependent. The rate of disappearance of leucocytes between 6 and 24 hours after irradiation was more rapid in the fish that received 5,000 R (Fig. 4). After 3 days the leucocyte numbers in fish that received 2,000 R began to recover but no recovery appeared in fish that received 5,000 R.

The leucocytosis observed in the pinfish after irradiation at both dose levels was more pronounced than in either goldfish or tench. This difference may reflect a reaction to the stress of radiation, since other types of stress cause leucocytosis in *Fundulus heteroclitus* (Slicher, 1961). The recovery in the leucocyte numbers of pinfish following a dose of 2,000 R carried the count above the mean control level but numbers then decreased. No recovery in leucocyte numbers was observed in the blood of either goldfish or tench following irradiation with doses higher than 1,500 R.

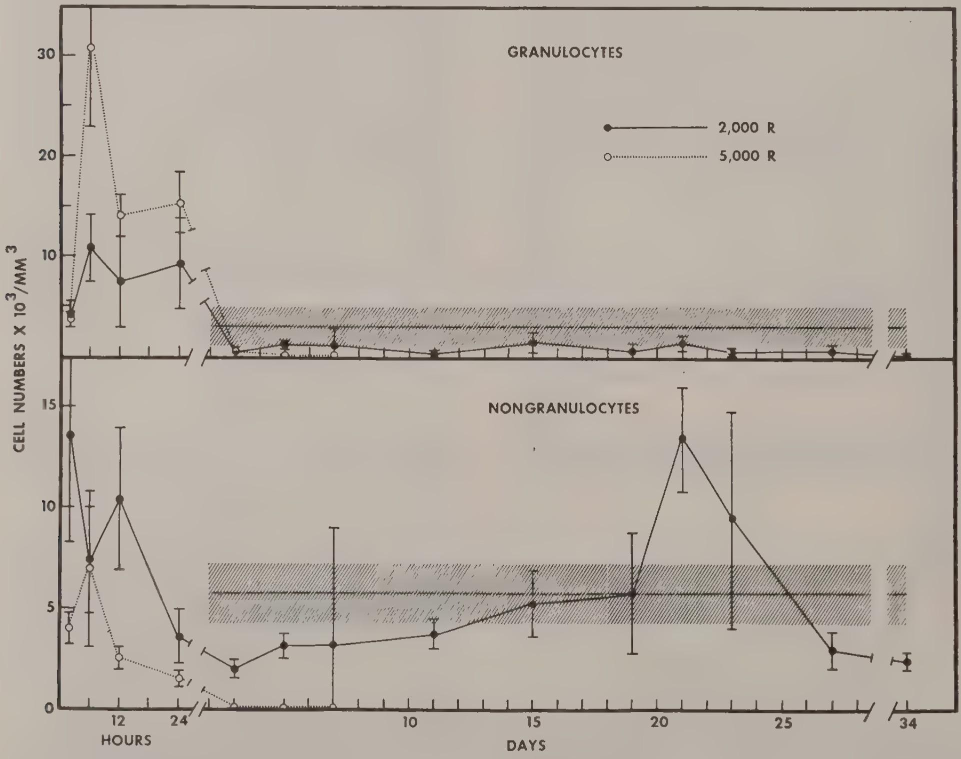

Fig. 5. Numbers of granulocytes and nongranulocytes in the blood of irradiated and unirradiated pinfish. Also see caption of Fig. 1.

Differential leucocyte counts on stained blood films revealed definite alterations in the proportions of granulated and nongranulated leucocytes in irradiated fish. Numbers of granulated leucocytes had the same general changes in the blood of pinfish irradiated with either 2,000 or 5,000 R (Fig. 5). Both groups of irradiated fish had some degree of granulocytosis during the 24 hours after irradiation. The greatest increase in granulocytes was 6 hours after irradiation in fish which received 5,000 R. After 6 hours, granulocyte numbers in both irradiated groups fell below the control level, where they stayed for the remainder of the experiment

Numbers of nongranulocytes in the blood of irradiated pinfish responded differently to radiation than did the granulocytes. Nongranulocyte counts were above the control level within 2 hours after irradiation and fish receiving 2,000 R had the larger number (Fig. 5). Although fluctuations occurred, by the 3rd day after irradiation, the numbers of nongranulocytes were below the control level in both groups of irradiated fish. The count of nongranulocytes in fish irradiated with 5,000 R remained low throughout the experiment, whereas some recovery appeared in fish irradiated with 2,000 R. In the group that received 2,000 R, nongranulocytes returned to the control level by the 15th day and surpassed the controls on the 21st day. From the 21st day through the 34th day, nongranulocytes decreased to the level of the 3rd day after irradiation. Thus it appeared from the differential counts that granulocytes were responsible for the leucocytosis in fish irradiated with 5,000 R, and that nongranulocytes were responsible for the overcompensation of leucocytes in fish that received 2,000 R.

Conclusions

The hematological responses discussed in this paper for irradiated pinfish are somewhat different from the changes reported for goldfish and tench. The primary differences in the response of irradiated pinfish are the resistance of the erythrocytic system to gamma radiation and the recovery of thrombocyte and leucocyte numbers following a radiation dose of 2,000 R. These data indicate that hematological radiation responses determined for any species cannot be extended to another.

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THE SCORPIONFISH SUBFAMILY SETARCHINAE, INCLUDING THE GENUS *ECTREPOSEBASTES*[1]

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ABSTRACT

The scorpionfish subfamily Setarchinae is revised on a worldwide basis. The subfamily is redefined and three genera and four species are recognized. *Lioscorpius longiceps* Günther is treated as a senior synonym of *Macroscorpius pallidus* Fowler after designation of a lectotype of the former. The genus *Ectreposebastes* Garman is referred to the subfamily, and *E. imus* Garman is reported for the first time from the Atlantic Ocean. Two species of *Setarches* are recognized, *S. longimanus* (Alcock) from the western Pacific and Indian oceans and *S. guentheri* Johnson from the Atlantic, Indian, and western Pacific oceans. Descriptions and a key are included.

INTRODUCTION

The scorpionfishes referable to the subfamily Setarchinae are few, but the systematic status of the 12 nominal species is poorly understood and has been complicated by erroneous and confounded descriptions. We recognize three genera and four species: *Lioscorpius longiceps* Günther, 1880 (replacing *Macroscorpius pallidus* Fowler, 1938) from the western Pacific; *Ectreposebastes imus* Garman, 1899, from the eastern Pacific and the Atlantic; *Setarches longimanus* (Alcock, 1894) from the western Pacific and Indian oceans; and *Setarches guentheri* Johnson, 1862, from the western Pacific, Indian, and Atlantic oceans. The affinities of the monotypic genus *Ectreposebastes* have not previously been reported; we refer it to the subfamily Setarchinae. *Scorpaenella cypho* Fowler, 1938, is also referred to this subfamily as a junior synonym of *Setarches longimanus*. The subfamily Setarchinae, established by Matsubara (1943), is redefined.

Fishes of this subfamily live offshore at depths of about 180-820 m. Stomach contents of two species suggest that they feed above the bottom, although all specimens except some of *Ectreposebastes imus* have been

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taken in large bottom trawls. Adults of *E. imus* have been collected in midwater trawls fished at 275-750 m over bottom depths of 915-2400 m.

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C. Richard Robins made suggestions at the onset of this work, and much of the first author's research in the preparation of this paper was supported by the National Science Foundation (NSF-GB-1350), C. Richard Robins, Principal Investigator. Material support was provided by a Bureau of Commercial Fisheries Fellowship. Travel to Africa for field work on the PILLSBURY and to England for examination of specimens in the British Museum (Natural History) was supported by the University of Miami Deep-Sea Biological Program sponsored by the National Geographic Society. Operation of the PILLSBURY was financed by a biological ship-time grant from the National Science Foundation (GB-1204).

METHODS

Terminology of bones and internal structures follows Matsubara (1943) and that of head spines follows Ginsburg (1953: 5-9). Measurements were taken with dial calipers as described by Eschmeyer (1965: 86-88). Measurements originating at the anterior end of the snout were taken from the most anterior end of the left premaxillary because of the presence of a variable notch at the junction of the premaxillaries. Pectoral-fin length was measured from the base of the upper ray to the tip of the fin. Head length was measured to the posterior margin of the opercular flap. Gill-raker counts on scorpaenid fishes are usually presented as total counts, but in the subfamily Setarchinae rudiments on the lower arch are indistinct or coalesced and were not counted. Rudiments on the upper arm are clearly distinguishable from gill rakers and are not included. The gill-raker formula used here represents the number of gill rakers on upper arch plus the number on lower arch equals total gill rakers (*e.g.*, 4 + 9 = 13).

Depositories of specimens are abbreviated as follows: ANSP—Academy of Natural Sciences of Philadelphia; BMNH—British Museum (Natural History), London; CNHM—Chicago Natural History Museum; MCZ—Museum of Comparative Zoology, Harvard University; SIO—Scripps Institution of Oceanography; SU—Division of Systematic Biology, Stanford University; TABL—Bureau of Commercial Fisheries Tropical Atlantic Biological Laboratory, Miami; UMML—University of Miami Marine Laboratory; USNM—United States National Museum, Washington, D. C.; and ZMC—Zoologiske Museum, Copenhagen.

Subfamily SETARCHINAE Matsubara

Diagnosis.—Lateral line a continuous trough covered by thin membranous scales. Scales small and cycloid. Cranium thin and cavernous, bones weakly ossified. Second suborbital bone uniformly broad or gradually becoming wider posteriorly, never T-shaped, and without spines in adults. Third and fourth suborbital bones absent. No fleshy appendages on head or body. Small slit present behind fourth gill arch. Vertebrae 24. Pyloric caeca 4 or 5.

Description.—Most spines not well developed, usually less prominent in large specimens. Parietal ridge low, ending in a spine or spinules posteriorly; nasal spine small but sharp; preocular, supraocular, and postocular spines present in small specimens, only preocular spine remaining as well defined spine in larger specimens. Other spines present on each side include the preorbital (3, first often small), preopercular (4 or 5) (Fig. 1), upper and lower post-temporal, supracleithral, cleithral, and pterotic. Suborbital bones (Fig. 2) usually lacking spinous points, small points sometimes present in small specimens. Swimbladder usually

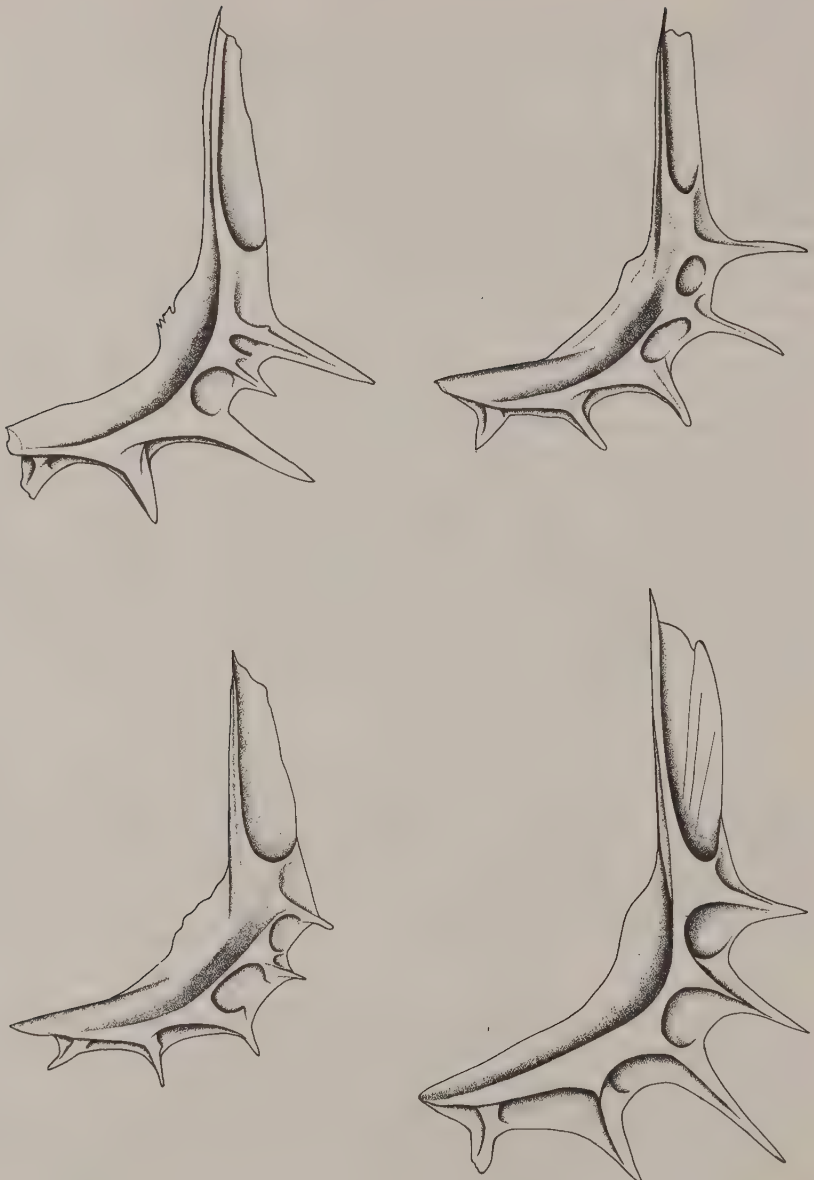

FIGURE 1. Preopercular bones of species of Setarchinae. Top, left to right: *Setarches longimanus, S. guentheri*. Bottom, left to right: *Lioscorpius longiceps, Ectreposebastes imus*.

present, greatly reduced or absent in *Ectreposebastes*. Stomach well pigmented, intestine and pyloric caeca sometimes pigmented. Dorsal spines XI-XIII, usually XII, the last spine at the leading edge of the second dorsal fin, rays 9-11 (last split to base); anal spines II-III, rays 4-6 (last split); pectoral rays 18-25, rays 2-3 to 15-18 branched in adults; pelvic rays I, 5; branchiostegal rays 7; developed gill rakers 2-5 + 8-11 = 10-15. Teeth present on premaxillary, dentary, vomer, pharyngeal, and palatine bones. Difference between developed gill rakers and rudiments distinguishable. Second and third lobes of preorbital bone ending in a moderate spine, first lobe with spine variable. Upper jaw length 21-28 per cent of standard length, head length 41-52 per cent.

Matsubara (1943: 359-362) gave a detailed discussion of the internal anatomy of the two species of *Setarches*. One section of his description must be changed, however. Matsubara (p. 360) stated, "It is very remarkable that in the present subfamily the basisphenoid is completely absent. . . ." He (p. 161) used the supposed absence of a basisphenoid and the fact that the second and third actinosts slightly intervene between the hypercoracoid and the hypocoracoid to conclude that ". . . the cottids have sprung off from a scorpaenid not very unlike the *Setarches*-ancestor." We found a small basisphenoid, connected only by cartilage, in cleared and stained specimens of all four species referred to the subfamily. Therefore Matsubara's conclusion is untenable. The Setarchinae is a highly specialized group in possessing such characters as the modified lateral line, reduced ossification, and reduction in head spines, and it is very unlikely that another group evolved from it.

Nomenclatural Remarks.—The subfamily Setarchinae was proposed by Matsubara in his classic monograph on the scorpaenoid fishes of Japan (1943); the subfamily name is based on the oldest and best known genus in the group, *Setarches* Johnson, 1862. Smith (1957a, b) has followed Matsubara. We have uncovered an earlier family-group name, Scorpaenellinae Fowler 1938. The complete description of his subfamily is given in his key to the genera of Philippine scorpaenids (1938a: 50-51) of which the following is the terminal couplet: "Scorpaenellinae, new subfamily. Dorsal spines 12, fin undivided; pectoral moderate, large, rays all simple, united; armature of head well developed . . . *Scorpaenella*." Characters such as "pectoral rays simple" and "armature of head well developed" are juvenile characters. Fowler based his new genus *Scorpaenella* on the species *S. cypho* which he described as new from one small specimen (20 mm SL). Fowler's species is a junior synonym of *Setarches longimanus* (Alcock). We have found no other specimens identified as *Scorpaenella cypho* and no subsequent use of his subfamily name. Because of the small size and relative unimportance of the subfamily, we do not feel that it is necessary, at the present time, to request

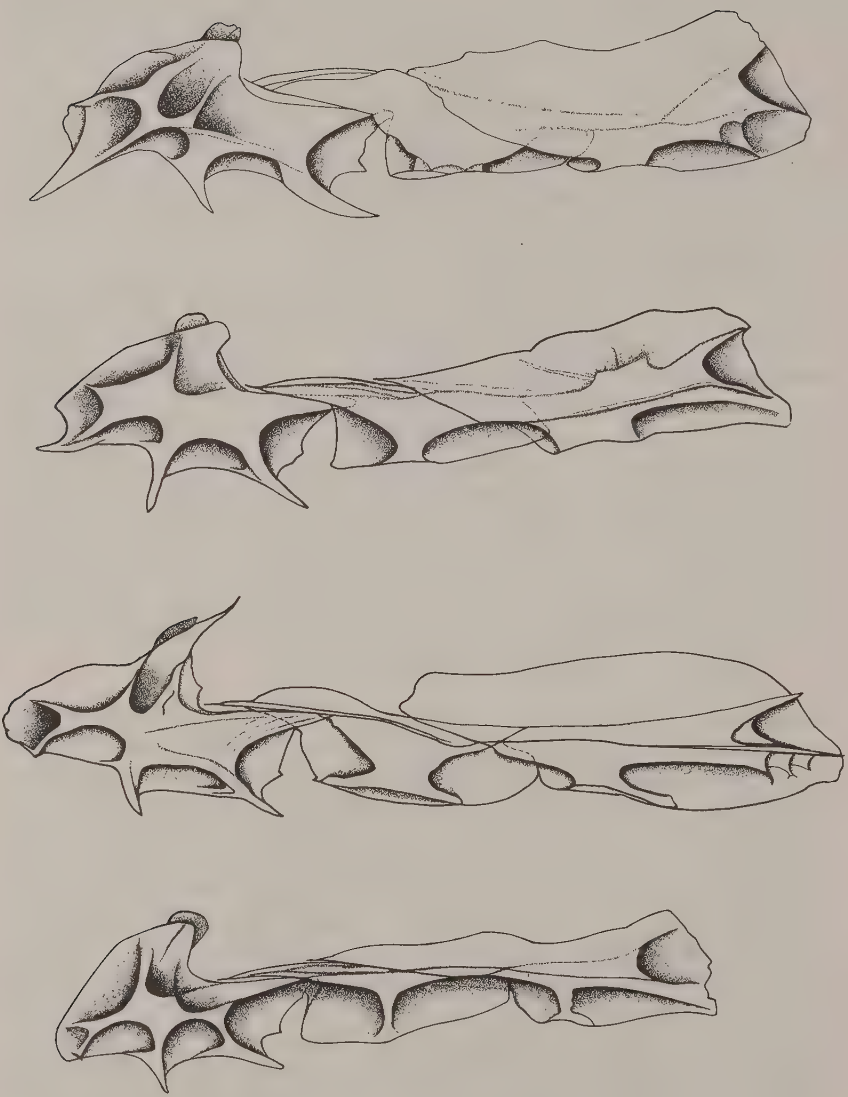

FIGURE 2. Suborbital bones of species of Setarchinae. From top to bottom: *Setarches longimanus, S. guentheri, Lioscorpius longiceps, Ectreposebastes imus.*

the International Commission on Zoological Nomenclature to use its plenary powers to suppress Scorpaenellinae Fowler in favor of Setarchinae Matsubara. We feel that Fowler's family-group name possibly could be rejected on the basis of Article 13(a)(i) of the International Code of Zoological Nomenclature, and could be rejected under the proposal now under consideration (Bulletin of Zoological Nomenclature, 1964), "Well-known and commonly used family-group names should prevail irrespective of . . . priority of group name. . . ."

KEY TO THE SPECIES OF SETARCHINAE

1. Anal spines II; body slender, greatest depth less than 28 per cent standard length; two or three dorsal spines before last spine very small, sometimes covered with scales (Fig. 3) *Lioscorpius longiceps* (p. 365)
1. Anal spines III; greatest body depth usually greater than 30 per cent standard length; two or three dorsal spines before last spine small, but at least one-fifth length of longest spine 2
2. Anterior preorbital spine much shorter than posterior two (Fig. 1); top of head with scales; pectoral rays 18-20; anal rays usually III, 6; orbit diameter contained about 2 times in interorbital; intestine and pyloric caeca pale; swimbladder rudimentary or absent .... *Ectreposebastes imus* (p. 367)
2. Anterior preorbital spine as long as posterior two (Fig. 1); top of head scaleless; pectoral rays 20-25; anal rays III, 5; orbit diameter subequal to interorbital; intestine and pyloric caeca black or gray; swimbladder well developed .... *Setarches* 3
3. Second preopercular spine reduced or absent, much shorter than first or third (Fig. 2); interorbital width 9-12 per cent standard length .... *Setarches longimanus* (p. 356)
3. Second preopercular spine subequal to or longer than first and third (Fig. 2); interorbital width 7-9 per cent standard length *Setarches guentheri* (p. 357)

Genus *Setarches* Johnson

Setarches Johnson, 1862: 177 (type species *Setarches güntheri* Johnson, 1862, by monotypy).

Bathysebastes Döderlein *in* Steindachner & Döderlein, 1884: 207 (type species *Bathysebastes albescens* Döderlein *in* Steindachner & Döderlein, 1884, by monotypy).

Lythrichthys Jordan & Starks, 1904a: 140 (type species *Lythrichthys eulabes* Jordan & Starks, 1904, by monotypy).

Scorpaenella Fowler, 1938a: 83-84 (type species *Scorpaenella cypho* Fowler, 1938, by original designation and monotypy).

Diagnosis.—Dorsal fin with XII (XI-XIII) spines and 9 or 10 (9-11) soft rays, fin deeply notched. Anal rays III, 5 (4-6), juveniles with only

2 anal spines. Pectoral rays 20-25. Preorbital bone with three moderate spines. Entire alimentary canal, including buccal cavity, stomach, pyloric caeca, and intestine black in life or gray-black in preservative. Swimbladder well developed. Greatest body depth 30-40 per cent of standard length.

Description.—The two species of *Setarches, S. guentheri* and *S. longimanus,* are very similar morphologically and in coloration of adults. Both species show the following changes with growth: larger specimens tend to have a proportionally less deep body, shorter head, shorter pectoral fin, and shorter spines in the dorsal fin. The internal features agree except that the extrinsic muscle band of the bladder is straight in *S. longimanus* and curved outward in *S. fidjiensis* [= *S. guentheri*] (Matsubara, 1943: 380).

Setarches longimanus (Alcock)

Lioscorpius longiceps, Günther, 1880: 52, Pl. 17, Fig. c (Philippine Is., CHALLENGER sta. 204; not of Günther, 1880: 40; see Discussion of Synonymy).—Wood-Mason & Alcock, 1891: 23 (not of Günther, 1880: 40; Andaman Sea, INVESTIGATOR sta. 115, 188-220 fms).

Lioscorpius longiceps, var. *longimanus* Alcock, 1894: Pl. 10, Fig. 3 (original description by reference to Wood-Mason & Alcock, 1891: 23; figure shows reduced preopercular spine).

Lythrichthys eulabes Jordan & Starks, 1904a: 140-141, Fig. 11 (original description; type locality off Ose Point, Suruga Bay, 60-70 fms, ALBATROSS sta. 3708).—1904b: 588, Fig. (compiled from type description; depth of type locality changed to 65-125 fms).

Scorpaenella cypho Fowler, 1938a: 84-85, Fig. 37 (original description; type locality March Is., Molucca Passage, 417 fms; juvenile; counts of pectoral and dorsal rays in error).—Herre, 1952: 443-444 (compiled from Fowler).—de Beaufort *in* Weber & de Beaufort, 1962: 63-64, Fig. 14 (description and figure from Fowler).

Setarches longimanus, Matsubara, 1943: 372-385, Figs. 129-135 (synonymy; recognized variety *longimanus* of Alcock as valid species; good description; figures showing variation; 29 specimens from Japan).—Kamohara, 1958: 56 and 1964: 74 (Suruga Bay to Kochi, Japan).

Setarches güntheri longiceps, de Beaufort *in* Weber & de Beaufort, 1962: 36-37, Fig. 7 (synonymy in part; description mostly based on *S. guentheri*).

Discussion of Synonymy.—Matsubara (1943: 372) was the first to recognize Alcock's *Lioscorpius longiceps* variety *longimanus* as a valid species. He included with question *Lioscorpius longiceps* Günther and on page 380 stated that *S. longimanus* agreed with the figure given by Günther but not with the description. Earlier authors (*e.g.,* Alcock, 1899: 28) also recognized this discrepancy. The specimen figured is *Setarches longimanus.* The specimen mentioned with the description given by Günther is designated lectotype of *Lioscorpius longiceps* (see Discussion of Synonymy for *Lioscorpius longiceps*).

Material Examined.—PHILIPPINE ISLANDS: BMNH 1879.5.14.193 (1, 72) CHALLENGER sta. 204, 115 fms.—USNM 136359-68, 136443-54, 135944-45 (40, 30-162) a combined lot labeled *S. longiceps*, ALBATROSS, Philippines; all individually tagged; one specimen each of *Scorpaena* sp., *Setarches guentheri,* and *Lioscorpius longiceps* removed; representative series of 24 specimens 30-162 mm SL counted and measured.

INDONESIA: USNM 98899 (1, 20) holotype of *Scorpaenella cypho* Fowler, 0°37′N, 127°15′E, 417 fms, ALBATROSS sta. D. 5618.

INDIAN OCEAN: USNM 189018 (5, 96-118), Andaman Sea, 10°39′N, 96°35′E, 384 m, ANTON BRUUN 23.—USNM 189017 (237, 46-109) not measured, and UMML 17374 (34, 48-82), Andaman Sea, 10°39′N, 97°06′E, 293 m, ANTON BRUUN 22a.

Diagnosis.—Second preopercular spine much shorter than first or third, or absent. Pectoral rays 21-23. Interorbital width greater than in *S. guentheri,* 8-12 per cent standard length versus 7-9 per cent.

Description.—Measurements and counts are summarized in Tables 1-8. No information is available on color in life, but it is presumably reddish, speckled with black. Color in preservative is specks of black or brown on a pale background. The specks in smaller specimens are more widely spaced, yielding a more pallid appearance. Color pattern and variation are shown by Matsubara (1943: Figs. 130-132).

Juveniles.—The smallest specimen available is the type of *Scorpaenella cypho* (20 mm SL). Some spines on the head are better developed at this size than in adults. The supraocular spine is well developed; the second preopercular spine is longer than in larger specimens. The parietal ridge is low, serrated on upper edge, and ending in two small points posteriorly (in larger specimens the parietal ridge is smooth and ends in one broad point). At 20 mm the first element in the second dorsal fin is still a soft ray; it changes to a spine at about 38 mm.

Distribution.—*Setarches longimanus* is known from a few localities in the western Pacific and Indian oceans. It has been reported from off the southeastern coast of Japan, the Philippine Islands, and the Andaman Sea. A wider distribution in the Indo-Pacific is suspected. Depths of capture of 23 ALBATROSS collections made in the Philippines vary from about 180 to 550 m (mean 362 m), plus one specimen from 704 m; the ANTON BRUUN took specimens at 293 and 384 m.

Setarches guentheri Johnson

Setarches güntheri Johnson, 1862: 177-179 (original description; type locality Madeira).—Alcock, 1899: 28-29 (included *Lioscorpius longiceps* Günther on basis of figure; included *S. remiger;* specimens from Andaman Sea in 185 and 188-220 fms, Bay of Bengal off Tricomali in 320-296 fms).—Brauer, 1908a: 294 (VALDIVIA stations 208 and 254, northwest coast of Sumatra and east coast of Africa).—Brauer, 1908b: 156, Pl. 33, Fig. 8 (structure of retina).—Weber, 1913: 491-493 (synonymy; specimens from Siboga stations 12, 74, 139, 251, 262, and 316).—Smith, 1934: 97-98, Pl. 6C (included *S. parmatus;* Natal).—Fowler, 1936: 929-930 (compiled).—Maul, 1948: 156 (Madeira).—Noronha & Sarmento, 1948: 123 (Madeira; common name "requeme de natura").—Cadenat, 1950: 321 (Congo).—Herre, 1952: 441 (compiled).—Herre, 1953: 573 (compiled).—Kuroda, 1952: 214-215 (color description).—Smith, 1957b: 85-86, Fig. 9 (included *S. marleyi;* specimens from points between St. Helena Bay, Cape (32°30′S, 17°30′E) and north of Durban at about 29°S).—Boutière, 1958: 12, et seq., Pl. 4 (coast of Morocco; life history notes).—Postel, 1959: 166 (listed).—Postel, 1960: 259 (listed as benthic species found between 200 and 250 m).

Setarches fidjiensis Günther, 1878: 179-180 (original description; type locality off Matuku, Fiji Islands in 215 fms).—Günther, 1887: 19 (wrongly lists as new species; description from Günther, 1878; footnote indicates type destroyed by artist).—Fowler, 1928: 292 (compiled).—Matsubara, 1943: 363-372, Figs. 126-128 (synonymy; good description and figures; compared with *S. marleyi* and *S. guentheri; S. parmatus* included in synonymy).—Kamohara, 1958: 56 and 1964: 74 (Tokyo to Kochi).

Setarches parmatus Goode, 1881: 480-481 (original description; type locality Fish Hawk sta. 876, 39°57′N, 70°56′W in 178 fms).—Goode & Bean, 1883: 213 (two specimens from Blake station 327 off North Carolina in 178 fms).—Jordan & Gilbert, 1882: 682 (compiled).—Jordan, 1885: 897 (listed).—Goode & Bean, 1896: 264-265, Fig. 249 (description; some records compiled; additional specimens from off Barbados in 209 fms, and off the Florida Panhandle).—Jordan & Evermann, 1898: 1860-1861 (compiled).—Jordan, Evermann, & Clark, 1930: 372 (listed).—Howell Rivero, 1936: 63 (Cuba).—Ginsburg, 1953: 97-100 (description; 42 specimens from western Atlantic at 98-280 fms).—Cervigón, 1963: 128 (Venezuela).

Bathysebastes albescens Döderlein *in* Steindachner & Döderlein, 1884: 207-208 (original description; type locality off Tokyo, Japan).—Günther, 1887: 20 (mostly compiled; 1 specimen from Sea of Japan).

Setarches albescens, Steindachner & Döderlein, 1887: 295, Pl. 1 (*Bathysebastes* placed in synonymy of *Setarches*).—Jordan & Snyder, 1901: 99 (listed).—Jordan & Starks, 1904a: 138-139 (brief synonymy; description; one specimen from Albatross sta. 3729, off Omai Point, Totomi, Japan).—Jordan & Starks, 1904b: 588 (compiled).—Shmidt, 1931: 108 (one specimen from Tokyo fish market; color description).

Setarches guentheri, Vaillant, 1888: 373-375 (description; Cape Verde Islands).—Norman, 1935: 33 (Atlantic).—Poll, 1959: 191-194, Fig. 69 (good description; stations 11, 16, 53, 154, and 203, off Angola and the Congo in 220-430 m).—Cadenat, 1961: 242 (listed as occurring in Senegal and Ghana).

Scorpaena remigera Gilbert & Cramer, 1897: 418-419, Pl. 40 (original description; type locality Hawaii, Albatross sta. 3476, 298 fms; USNM 47726).

Setarches remiger, Gilbert, 1905: 634 (corrected original description; additional specimens from 14 more Albatross stations around the Hawaiian Islands).—Fowler, 1928: 291-292 (compiled).—Fowler, 1938b: 290 (listed).

Setarches marleyi Fowler, 1935: 398, Figs. 28-29 (original description; type locality Natal; ANSP 63797).—Norman, 1939: 93 (Zanzibar; Murray Exp. sta. 115 and 122; suggestion of one Indo-Pacific species of *Setarches*—*S. longiceps; S. parmatus* apparently a synonym of *S. guentheri*).

Setarches longiceps, Smith, 1949: 370 (figure 1036; description), (also in 1953 and 1961 editions).

Setarches güntheri longiceps, de Beaufort *in* Weber & de Beaufort, 1962: 36-37, not Fig. 7 (synonymy in part; description of *S. guentheri;* figure from Günther, 1880, is *S. longimanus*).

Discussion of Synonymy.—Various authors have suggested previously that only one species occurred in the Indian and Atlantic oceans, in the Pacific and Atlantic, or from the Pacific to the Atlantic. De Beaufort (1962) treated all *Setarches* from the Pacific and Indian oceans as a subspecies of *S. guentheri* on Norman's (1939) suggestion that all the Indo-Pacific forms were conspecific. Matsubara (1943) included the western Atlantic species *S. parmatus* with *S. fidjiensis* in the Pacific but separated *S. guentheri* from *S. fidjiensis*. The characters used by Matsubara to distinguish *S. guentheri* from *S. fidjiensis* are related to the size of specimens, with the exception of the two pyloric caeca reported in the original description of *S. guentheri* (Johnson, 1862: 179). Dr. P. H. Greenwood has kindly reexamined the type and has found it to have four pyloric caeca like all our other specimens.

The species does round the tip of South Africa, and no permanent barriers exist between the populations. Therefore, despite geographic variation, we recognize only one species with a distribution from Hawaii to the western Atlantic Ocean.

Material Examined.—HAWAII: USNM 47726 (1, 83) holotype, and USNM 75828 (1, 63) and SU 4917 (1, 64) paratypes of *Scorpaena remigera,* ALBATROSS 3476.—USNM 125515 (4, 107-129).—USNM 55251 (8, 52-120).—CNHM 55993 (1, 120).—SU 8572 (3, 74-123).

PHILIPPINES: USNM 136360 (1, 96).

JAPAN: USNM 50910 (1, 36) holotype of *Lythrichthys eulabes,* Suruga Bay.—SU 7177 (1, 177) Okinose.

INDIAN OCEAN: ANSP 63797 (1, 191) holotype of *Setarches marleyi,* Natal.—USNM 109508 (1, 203) Zanzibar, John Murray Expedition.

EASTERN ATLANTIC: BMNH 1867.4.22.36 (1, 180) holotype of *Setarches güntheri,* Madeira.—BMNH 1936.3.25.1 (1, 180) Madeira.—UMML 15690 (4, 47-80) 4°56′N, 5°01′W, 270-180 fms, PILLSBURY 51.—UMML 15603 (24, 45-75) 4°40′N, 9°20′W, 200-170 fms, PILLSBURY 73.—USNM 198214 (2, 50-74) 4°25′N, 8°29′30″W, 400 m, GTS I, trans. 18, sta. 8, BBC 844.—USNM 198213 (4, 41-45) 4°36′N, 9°15′W, 400 m, GTS I, trans. 17, sta. 8, BBC 851.—USNM 198212 (14, 45-82) 5°17′N, 9°55′W, 400 m, GTS I, trans. 16, sta. 8, BBC

TABLE 1
Number of Dorsal Rays in Species of Setarchinae

Species	Spines			Soft rays		
	11	12	13	9	10	11
Lioscorpius longiceps	–	27	–	1	26	–
Ectreposebastes imus	–	36	–	5	32	–
Setarches longimanus	1	60	1	3	56	3
Setarches guentheri						
Hawaii	–	22	–	1	21	–
Japan[1]	1	145	–	8	137	1
Philippines	–	1	–	–	1	–
Zanzibar	–	1	–	–	1	–
Eastern Atlantic	3	63	3	25	48	–
Western Atlantic	–	66	–	19	47	–

[1] Calculated from Matsubara, 1943: 369.

TABLE 2
Number of Anal Rays in Species of Setarchinae

Species	Spines		Soft rays			
	2	3	4	5	6	7
Lioscorpius longiceps	26	–	–	–	26	–
Ectreposebastes imus	–	36	–	1	35	1
Setarches longimanus	–	25	3	60	1	–
Setarches guentheri	–	125	4	154	95	–

TABLE 3
Number of Left Pectoral Rays in Species of Setarchinae

	17	18	19	20	21	22	23	24	25
Lioscorpius longiceps	–	–	–	–	–	–	4	16	7
Ectreposebastes imus	–	12	19	5	–	–	–	–	–
Setarches longimanus	–	–	–	–	11	48	4	–	–
Setarches guentheri									
Hawaii	–	–	–	3	13	1	–	–	–
Japan[1]	–	–	–	x	xx	xx	x	–	–
Philippines	–	–	–	–	–	1	–	–	–
Zanzibar	–	–	–	–	–	1	–	–	–
Eastern Atlantic	–	–	–	–	5	46	16	1	–
Western Atlantic	–	–	–	–	–	8	46	10	1

[1] Matsubara (1943: 364) gives range of 20-24, mode of 22, and mean of 21.62 for 146 Japanese specimens.

857.—USNM 198211 (11, 42-83) 6°08′N, 10°57′W, 350-400 m, GTS I, trans. 14, sta. 8, BBC 868.—USNM 198210 (14, 52-97) 6°31′N, 11°29′W, 350-500 m, GTS I, trans. 13, sta. 8, BBC 887.—USNM 199452 (1, 40) 1°56′S, 8°47′E, 300 m, GERONIMO 204.—USNM 199453 (2, 60-85) 2°00′S, 8°46′E, 458-613 m, GERONIMO 206.—USNM 199451 (4, 40-48) 3°02′S, 9°21′E, 300 m, GERONIMO 220.—USNM 199454 (1, 49) 3°31′S, 9°53′E, 400 m, GERONIMO 228.—ANSP 103306 (6, 55-136) 3°32′S, 9°53′E, 400 m, GERONIMO 229.—MCZ 44403 (6, 46-118) 4°03′S, 0°22′E, 300 m, GERONIMO 237.—USNM 199455 (5, 54-143) 4°07′S, 10°23′E, 400 m, GERONIMO 238.—CNHM 73380 (6, 53-129) 4°38′S, 11°02′E, 400 m, GERONIMO 247.—ZMC uncat. (761, 40-156) 2°09′N, 9°27′E, 530-850 m, ATLANTIDE 120 [not measured].

WESTERN ATLANTIC: USNM 28084 (1, about 41) holotype of *Setarches parmatus*, 39°57′N, 70°56′W, 120 fms, FISH HAWK 876.—UMML 11330 (2, 91-105) 25°29′-33′N, 79°54.5′-80°02′W, 180-185 fms, GERDA 77.—UMML 12505 (4, 89-122) 29°12′N, 86°42′W, 225 fms, OREGON 4073.—UMML 13493 (3, 55-75) 24°29′N, 83°29′W, 190 fms, OREGON 4335.—UMML 12508 (5, 53-94) 29°22′N, 86°48′W, 245 fms, OREGON 4072.—UMML 13508 (8, 39-187) 11°46′N, 69°15′W, 240 fms, OREGON 4417.—UMML 14263 (4, 110-189) 11°46′N, 69°16′W, 240 fms, OREGON 4418.—UMML 5038 (3, 77-158) 27°53′N, 79°09′W, 375-415 fms, SILVER BAY 442.—UMML 7314 (1, 123) 11°40′N, 62°40′W, 215 fms, OREGON 2770.—UMML 2254 (3, 39-53) 32°15′N, 78°51′W, 190 fms, COMBAT 300.—UMML 12507 (1, 59) 29°04′N, 88°27′W, 200 fms, OREGON 4043.—UMML 13975 (1, 83) 24°28′N, 83°28′W, 205 fms, OREGON 4354.—UMML 13672 (1, 49) 24°28′N, 83°26′W, 210 fms, OREGON 4368.—UMML 14018 (1, 68) 10°54′N, 67°08′W, 220 fms, OREGON 4453.—UMML 12511 (1, 61) 29°05′N, 88°30′W, 210 fms, OREGON 4331.—UMML 12509 (4, 47-58) 29°11′N, 88°06.5′W, 200 fms, OREGON 3677.—ANSP 101191 (1, 54) 11°34′N, 62°49′W, 160-200 fms, OREGON 2781.—UMML 15365 (1, 109) 11°09.5′N, 72°25′W, 160 fms, OREGON 4858.—SU 50187 (3, 51-61) 1°49′N, 46°48′W, 225 fms, OREGON 2083.—UMML 16195 (11, 47-149) 11°30′N, 60°46′W, 200-240 fms, OREGON 5028.—UMML 17327 (4, 58-84) 29°40′N, 80°12′W, 200 fms, OREGON 5089.—UMML 16268 (5, 57-90) 11°31′N, 60°51′W, 240-250 fms, OREGON 5029.—UMML 17310 (1, 134) 29°45′N, 80°13′W, 188 fms, OREGON 5075.—UMML 17325 (7, 100-154) 29°43′N, 80°11′W, 192 fms, OREGON 5081.—UMML 12384 (2, 98-109) 25°31′N, 79°57′W, 200 fms, GERDA 66.

Diagnosis.—Second preopercular spine well developed, subequal or longer than first and third. Pectoral rays 20-25, modally 21 in Hawaii, 22 in

TABLE 4

BODY DEPTH EXPRESSED AS A PERCENTAGE OF STANDARD LENGTH IN SPECIES OF SETARCHINAE[1]

Species	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37
Lioscorpius longiceps	4	3	5	5	2	2	–	1	–	–	–	–	–	–	–	–	–
Ectreposebastes imus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	4
Setarches longimanus	–	–	–	–	–	–	–	–	–	–	2	7	5	9	11	8	1
Setarches guentheri	–	–	–	–	–	–	–	2	3	4	6	14	25	19	19	14	8

	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	N	$\bar{X}$
Lioscorpius longiceps	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	22	23.4
Ectreposebastes imus	4	2	4	1	–	1	3	1	2	1	2	2	–	–	1	28	42.3
Setarches longimanus	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	45	34.3
Setarches guentheri	4	2	2	–	–	–	–	–	–	–	–	–	–	–	–	122	34.0

[1] Relative depth of body tends to decrease in larger specimens.

eastern Atlantic, and 23 in the western Atlantic. Interorbital width less than in *S. longimanus,* 7-9 per cent versus 8-12 per cent standard length.

Description.—Measurements and counts are presented in Tables 1-8. In life, specimens are brick red to orange with reddish black specks on the head and body. Smaller specimens are usually reddish gray with black specks. The smallest specimens (about 40 mm) have the dark pigment more concentrated in a patch above the pectoral fin, and below the soft dorsal fin, with less pigment on the caudal peduncle.

Variation.—Counts and measurements vary geographically. Specimens from Hawaii average lower in number of pectoral rays (Table 3), but the number of pectoral rays increases to the west; the average is highest in the western Atlantic. Specimens from Hawaii average higher in number of soft dorsal rays (Table 1); this count decreases to the west, but the population in the western Atlantic has a slightly higher mean than that in the eastern Atlantic. The pectoral-fin length is greatest in specimens from Hawaii.

Despite geographic variation, no subspecies are recognized. The populations appear to be more or less continuous, and have a wide north-south distribution. The species occurs at the tip of South Africa.

Distribution.—As recognized here, *S. guentheri* occurs from Hawaii west to the western Atlantic. It has also been reported from Fiji, the Andaman Sea, the Bay of Bengal, the Sea of Japan, the southeast coast of Japan, Zanzibar, north of Durban, Natal, the Gulf of Guinea, the Cape Verde Islands, Senegal, Morocco, and Madeira. This species has the widest distribution of any known scorpaenid.

S. guentheri is widely distributed in the western Atlantic from 39°57′N, 70°56′W (type of *S. parmatus*) to northern Brazil (OREGON 2082). The Bureau of Commercial Fisheries Exploratory Fishing and Gear Research Base at Pascagoula, Mississippi, presently has 274 records of *Setarches guentheri* from the western Atlantic. We have verified identification of specimens from 69 of these stations and are confident that the majority of the others are accurate.

Ecology.—Several authors (*e.g.,* Herre, 1952; Wood-Mason & Alcock, 1891) have reported species of *Setarches* as being benthic or pelagic. We can find no records of the capture of *S. guentheri* by means other than bottom trawls. An analysis of 274 Bureau of Commercial Fisheries records for *S. guentheri* in the western Atlantic Ocean shows a depth range of about 220 to 685 m (mean 390 m) and a bottom temperature range of 42-55°F (5.5°-12.5°C) (mean 49.6°F [9.5°C] for 91 stations). Nearly two-thirds of the 29 records from the Gulf of Guinea are at 400 m. This is partly because the two deepest stations of each transect of the Guinean

TABLE 5

Pectoral-Fin Length Expressed as a Percentage of Standard Length in *Setarches guentheri*

Locality	31	32	33	34	35	36	37	38	39	40	41	42	43	44	N	X̄
Hawaii	–	–	–	–	–	1	3	4	3	3	1	1	1	–	17	38.9
Eastern Atlantic	5	7	13	13	11	4	5	2	4	–	1	2	–	1	68	34.8
Western Atlantic	1	1	11	14	14	11	6	4	3	–	1	–	–	–	66	35.2

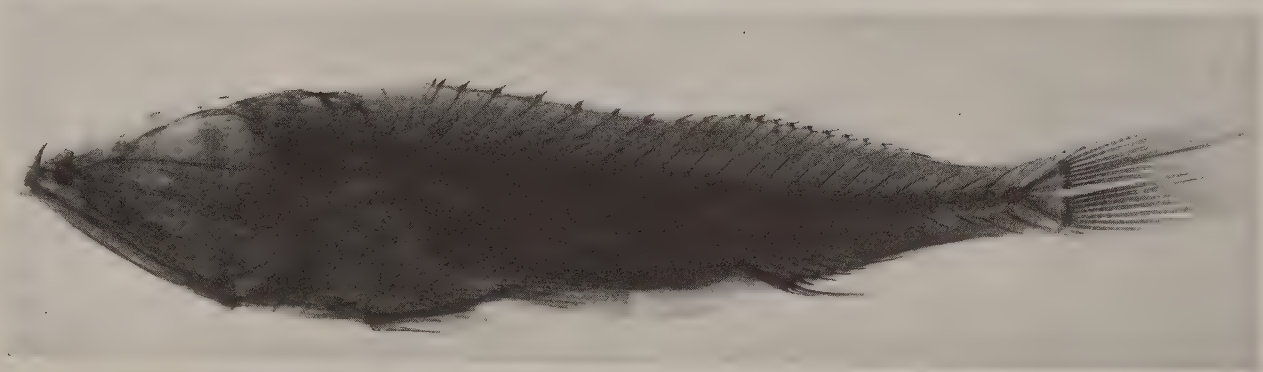

Figure 3. Radiograph of holotype of *Macroscorpius pallidus* (= *Lioscorpius longiceps*). USNM 98890, 130 mm standard length.

Trawling Survey were at 200 m and at 400 or 600 m (Williams, 1964). *S. guentheri* was not collected at the 200 m station. For five stations Poll (1959) gave the abundance of *S. guentheri*: 220-240 m, 2 specimens; 300-310 m, 4; 350-380 m, 7; 290-390 m, 76; and 400-430 m, 115. This tends to confirm that *S. guentheri* prefers a depth of about 400 m. Specimens usually arrive at the surface with the stomach everted, but four from the western Atlantic had partially digested material in the stomach. Two specimens contained parts of crustaceans of the bathypelagic caridean family Oplophoridae, one contained parts of *Oplophorus* sp., and the fourth an amphipod. Therefore, it is suggested that this species feeds in the water column though it lives on or just off the bottom.

Genus *Lioscorpius* Günther

Lioscorpius Günther, 1880: 40-41 (type species *Lioscorpius longiceps* Günther, 1880, by monotypy).

Macroscorpius Fowler, 1938a: 75 (type species *Macroscorpius pallidus* Fowler, 1938, by original designation and monotypy).

Diagnosis.—Preorbital bone with first spine greatly reduced. A long dorsal projection covers dorsal articulating surface of preorbital. Anal rays II,6. Pectoral rays 23-25. Last 2-3 dorsal spines in first dorsal fin small and frequently buried (Fig. 3). Swimbladder well developed with large gas gland. Body depth less than in other species of Setarchinae, 21-28 per cent standard length. Interorbital region narrow, only 6-7 per cent standard length.

Lioscorpius longiceps Günther

Lioscorpius longiceps Günther, 1880: 40-41 (original description; type locality Ki [now Kai] Islands, Arafura Sea, CHALLENGER sta. 192, 129 fms; not p. 52 or Pl. 17, Fig. c, which are referable to *Setarches longimanus*).—Günther, 1887: 20 (listed).—Goode & Bean, 1896: 265 (compiled).—Jordan & Richardson, 1910: 51 (listed).

Macroscorpius pallidus Fowler, 1938a: 76-77, Fig. 33 (original description; type locality Point Tagola Light, 8°48′N, 123°31′E, northern Mindanao and vicinity in 200 fms, also series from the Philippines in 162-226 fms).—Matsubara, 1943: 386-388, Fig. 136 (one specimen from Shikoku Is., Japan in 100 fms).—Herre, 1952: 439-440 (description from Fowler & Matsubara).—Herre, 1953: 565 (listed).—Kamohara, 1958: 56 and 1964: 74 (Wakayama Pref. to Kochi, Japan).

Discussion of Synonymy.—Two specimens were located in the British Museum (Natural History) bearing the name *Lioscorpius longiceps*. One, BMNH 1879.5.14.199, is of the length and bears the locality data (Ki Islands) given by Günther (1880: 40) for the specimen mentioned with his description of the species. Data in the bottle containing the other specimen, BMNH 1879.5.14.193, match the data given by Günther on page 52 of the same work as "*Lioscorpius longiceps* n. sp. (see p. 40).

TABLE 6

SNOUT LENGTH EXPRESSED AS A PERCENTAGE OF STANDARD LENGTH IN SPECIES OF SETARCHINAE

Species	10	11	12	13	14	15	16	17	N	X
Lioscorpius longiceps	–	–	1	16	4	1	–	–	22	13.2
Ectreposebastes imus	–	–	–	5	15	9	–	1	30	14.2
Setarches longimanus	2	11	24	4	3	3	–	–	47	12.1
Setarches guentheri	1	22	46	39	7	–	–	–	115	12.3

Station 204, Philippines." The description includes data from both specimens. The dorsal spine count of "8 or 9/11" matches the Ki specimen (the 9th through 11th spines are tiny and covered at least partially with scales; all 12 spines are clearly visible in the figured specimen); anal rays $\frac{\text{“2 or 3”}}{6}$ fit the Ki specimen (II,6) better than the Philippine specimen (III,5); body depth is given as one-fourth standard length in the description, fitting the Ki specimen, and is represented as about one-third in the figure, fitting the Philippine specimen. We select the Ki specimen, BMNH 1879.5.14.199, as lectotype, which makes *Macroscorpius pallidus* Fowler 1938 a junior synonym of *Lioscorpius longiceps* Günther 1880. The figured specimen from the Philippine Islands is referred to *Setarches longimanus.*

Material Examined.—BMNH 1879.5.14.199 (1, 85) lectotype of *Lioscorpius longiceps,* Ki [Kai] Islands.—USNM 98890 (1, 130) holotype of *Macroscorpius pallidus,* Mindanao, Philippines.—USNM 113004 (9, 88-114) and 98995 (15, 104-135) paratypes of *M. pallidus,* Philippine Islands.—USNM 98989-94 and 98996-99006 and SU 40201 (3), all paratypes of *M. pallidus,* checked for identification but no counts or measurements taken; all from the Philippines except 98991 from Borneo.—USNM 136449 (1, 63) Philippines, ALBATROSS.

Description.—Measurements and counts are presented in Tables 1-8. Matsubara (1943: 387) reported the color in life as pink, with five indefinite large dark blotches on the sides of the body, the first three below the spinous dorsal, one below the soft dorsal, and one on the base of the caudal fin.

Distribution.—The species is known from the Philippines, Borneo, Japan, and the Arafura Sea. It is found at depths of about 180 to 410 m.

Genus *Ectreposebastes* Garman

Ectreposebastes Garman, 1899: 53 (type species *Ectreposebastes imus* Garman, 1899, by monotypy).

TABLE 7

Interorbital Width Expressed as a Percentage of Standard Length in Species of Setarchinae

Species	6	7	8	9	10	11	12	13	14	15	N	$\bar{X}$
Lioscorpius longiceps	13	9	–	–	–	–	–	–	–	–	22	6.4
Ectreposebastes imus	–	–	–	–	1	1	5	19	4	1	31	12.9
Setarches longimanus	–	–	13	9	10	11	2	–	–	–	45	9.6
Setarches guentheri	–	1	60	65	–	–	–	–	–	–	126	8.5

Diagnosis.—Preorbital bone with anterior spine greatly reduced. Anal rays III,6; juveniles with only 2 anal spines. Pectoral rays 18-20. Pyloric caeca 5. Stomach often with some black pigment, but intestine and pyloric caeca unpigmented. Swimbladder absent or rudimentary. Body soft and flabby in life. Body depth averages greater than in other genera of Setarchinae, 37-52 per cent of standard length.

Ectreposebastes imus Garman

Ectreposebastes imus Garman, 1899: 53-55, Pls. 8, 9, and 71, Fig. c (original description; type locality Galapagos Islands, 384 fms, Albatross 3403).—Fowler, 1938b: 257 (listed).

Material Examined.—Eastern Pacific: MCZ 28766 (3, 113-117, 2 partially dissected) and USNM 153606 (1, 90) syntypes of *Ectreposebastes imus*, off Galapagos Islands, 0°58′30″S, 89°17′W, 384 fms, Albatross 3403.—USNM 135641 (1, 116) and SU 25619 (1, 101) 0°29′S, 89°54′30″W, 392 fms, Albatross 2818.—USNM 169165 (1, 113) 0°37′S, 80°00′W, 401 fms, Albatross 2792.

Western Atlantic: USNM 198219 (1, 51) 29°06′N, 88°02′W, 150 fms, over bottom depth of 500 fms, Oregon 3219.—CNHM 66455 (1, 59), and USNM 199467 (1, 60) 16°41′N, 82°26′W, 375-450 fms, Oregon 1940.—USNM 188875 (3, 55-64) 9°02.4′N, 76°31.5′W, 400 fms, Oregon 4902.

Eastern Atlantic: UMML 15691 (1, 171) 4°24′-30′N, 3°00′-06′W, 300 m over bottom depth of 1200-1340 fms, Pillsbury 39.—UMML 15692 (6, 68-139) 4°20′-30′N, 9°26′-22′W, 350-400 fms, Pillsbury 74.—UMML uncat. (1, about 160) 2° 45′-49′N, 8°45.9′-42.6′E, 750 m over bottom depth of 965-1015 fms, Pillsbury 261.—USNM 198215 (4, 56-82) 9°10′N, 15°39′W, 600-610 m, GTS I, trans. 6, sta. 8, BBC 941.—USNM 198216 (5, 69-127), MCZ 44401 (1, 82), CNHM 73379 (1, 82), and SIO 65-430-53A (1, 74), 6°31′N, 11°29′W, 350-500 m, GTS I, trans. 13, sta. 8, BBC 887.—USNM 198217 (5, 72-132) 5°38′N, 10°26′W, 560-640 m, GTS I, trans. 15, sta. 8, BBC 866.—USNM uncat. (1, 121) 4°37.5′N, 9°15′W, 400 m, GTS II, trans. 17, sta. 8.

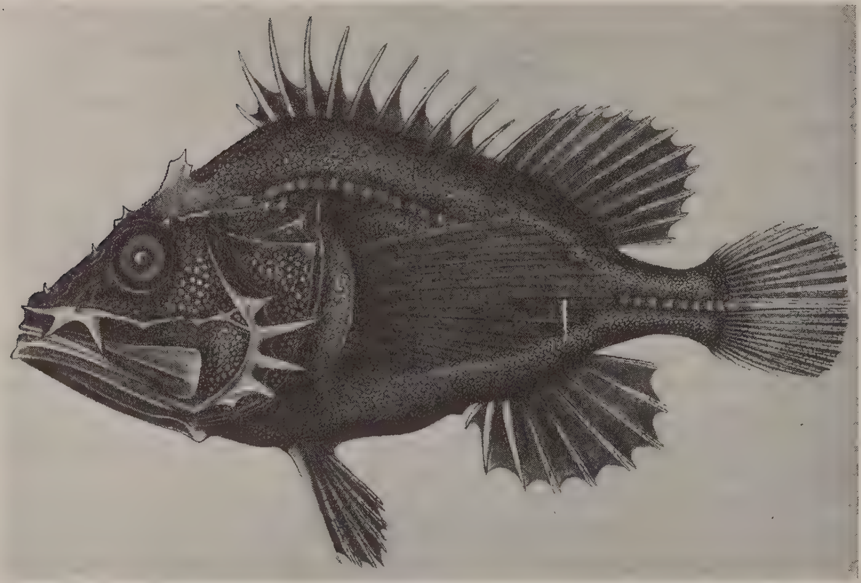

FIGURE 4. *Ectreposebastes imus.* USNM 198215, Gulf of Guinea, Guinean Trawling Survey, 55.5 mm standard length.

The following larval specimens were studied: UMML 18227 (1, 16) south of Puerto Rico, 17°31′-25′N, 66°33′-55′W, 165 m over bottom depth of about 2000 fms, GERDA Carib. 4.—UMML 18228 (1, 15) 3°30′N, 4°51′-52′E, 400 m over about 2000 fms, PILLSBURY 306.

Description.—Measurements and counts are presented in Tables 1-8. The measurements show more variation than is present in the other species, but this is not correlated with geography and is probably due to the flabby body and poor ossification. In alcohol the body behind the head shrinks to about half its width in life. The body is black in small specimens (pale where scales are rubbed off) and maroon and black in adults (Fig. 4). The buccal cavity is black with patches of bright orange and red in life; the pharyngeal teeth are red or orange.

Larvae.—Two small specimens, 15 and 16 mm standard length, are unpigmented. The smaller specimen in life had the pectoral fin yellow with pink at the distal margin, and the body had slight tinges of pink. The peritoneum was silver. Head spines are better developed than in larger specimens. A pair of long, serrated parietal spines, almost twice the orbit diameter, is present. A small spine is present at the base of each long spine in one specimen. (In larger specimens the base of each long parietal spine is still present (see Fig. 4).) Of the ocular spines, the supraocular spine is best developed and has a few serrations on its edges. The pectoral fin reaches to the posterior end of the anal fin base; the rays are undivided. There are only 11 dorsal spines at this stage; the one at the beginning of the soft-rayed portion is still in the condition of a soft ray. The third anal element has not yet changed from a soft ray to a spine. The head is about 45 per cent of standard length and the body depth about 50 per cent.

Distribution.—*Ectreposebastes imus* was known from only three ALBATROSS stations in the tropical eastern Pacific at the Galapagos Islands and off the coast of Peru. Specimens in this study extend the range to both sides of the Atlantic Ocean (Fig. 5). *E. imus* is apparently able to survive in midwater.

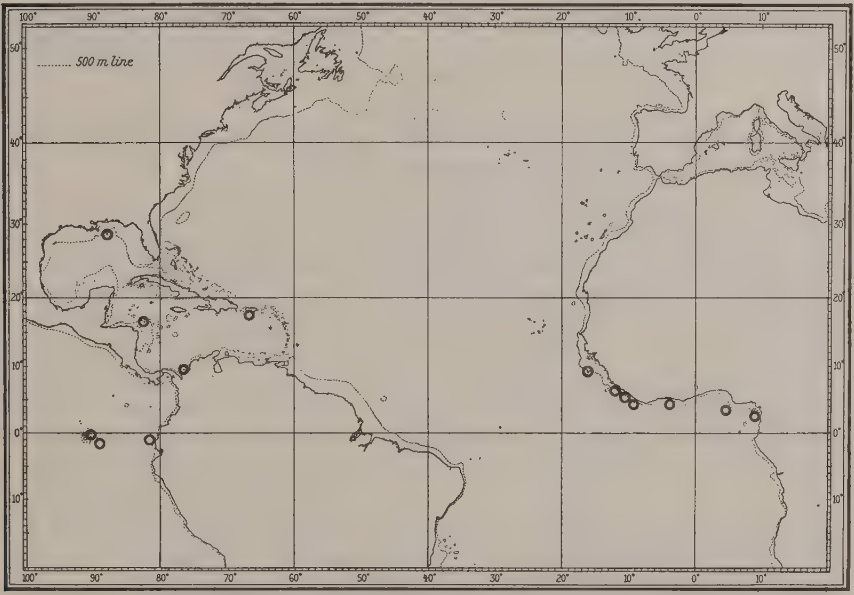

FIGURE 5. Range of *Ectreposebastes imus.*

Ecology.—Most specimens of *E. imus* have been taken in large bottom trawls fished at 500 to 800 m. In the Gulf of Guinea during Guinean Trawling Survey I, specimens were collected at two out of four stations at least 500 m deep. A station at 350-500 m produced 8 specimens of *E. imus* and 18 of *Setarches guentheri.* Three adults of *Ectreposebastes* have also been taken in midwater trawls: a specimen 51 mm SL by the

TABLE 8

PREDORSAL DISTANCE EXPRESSED AS A PERCENTAGE OF STANDARD LENGTH IN SPECIES OF SETARCHINAE

Species	36	37	38	39	40	41	42	43	44	45	46	47	48	49	N	$\overline{X}$
Lioscorpius longiceps	2	4	2	6	3	5	–	–	–	–	–	–	–	–	22	38.9
Ectreposebastes imus	–	–	–	–	–	1	2	3	4	4	3	4	4	5	30	45.8
Setarches longimanus	–	1	–	3	9	12	6	9	3	1	–	–	–	–	44	41.4
Setarches guentheri																
Hawaii	–	–	–	–	2	3	3	4	5	1	–	–	–	–	18	42.6
Eastern Atlantic	–	1	2	4	13	20	13	13	3	–	–	–	–	–	69	41.2
Western Atlantic	3	10	7	14	8	7	9	5	2	–	–	–	–	–	65	39.7

OREGON (station 3219) in a 60-foot midwater trawl fished at 275 m over a bottom depth of 915 m, and specimens of 171 and 160 mm by the PILLSBURY (stations 39 and 261) in 10-foot Isaacs-Kidd midwater trawls fished at 300 m and 750 m over bottom depths of about 1800 to 2400 m.

Of all scorpionfishes, *E. imus* is structurally the best adapted to life in midwater. The swimbladder is absent or rudimentary. The bones are poorly ossified, and spines are weak and usually broken during capture. The scales are thin and deciduous. The white body musculature is soft and flabby.

It is unlikely that up to eight specimens per bottom tow could be taken from midwater while the trawls were being set or retrieved, but stomach contents suggest that regardless of the position of the fish in relation to the bottom, they do not feed on the bottom. Of the six specimens from PILLSBURY station 74 (bottom tow), three contained identifiable stomach contents; one had parts of crustaceans; a second an amphipod and parts of a midwater shrimp, *Sergestes* sp.; and the third had three specimens of *Sergestes* sp.

SUMARIO

SUBFAMILIA DE PECES RASCACIOS, SETARCHINAE, INCLUYENDO EL GÉNERO *Ectreposebastes*

La pequeña subfamilia de peces rascacios Setarchinae es revisada sobre bases mundiales; se reconocen tres géneros y cuatro especies. El género monotípico *Ectreposebastes* es colocado en Setarchinae y *E. imus* Garman, conocido en el Pacífico Oriental, en las Islas Galápagos y la costa del Perú, es reportado en el Atlántico Oriental y Occidental. *Setarches guentheri* Johnson se encuentra en toda la zona circuntropical excepto en el Pacífico Oriental, aunque algunos conteos y medidas varían geográficamente. *Setarches longimanus* Alcock está presente en el Pacífico Occidental y Océano Índico. *Lioscorpius longiceps* Günther (en lugar de *Macroscorpius pallidus* Fowler) es conocido en el Océano Pacífico Occidental. Se incluyen descripciones y claves.

Los peces de esta subfamilia viven lejos de la costa a profundidades alrededor 180-820 m, pero se conoce poco de su ecología. El contenido estomacal de dos especies sugiere que se alimentan sobre el fondo, aunque todos los ejemplares excepto algunos de *Ectreposebastes imus* han sido cogidos en rastreos del fondo. Adultos de *E. imus* han sido recolectados en media agua de 275-750 m sobre fondos de 915-2400 m de profundidad.

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BERING SEA

The Bering Sea, which lies between latitudes 51°N and 66°N, and longitudes 157°W and 163°E, is usually considered an extension of the North Pacific Ocean. Having an area of 2.3×10^6 km^2, a volume of 3.7×10^6 km^3 and an average depth of 1636 meters, it is the second largest of the relatively confined seas; the Mediterranean Sea being the largest. Its configuration at sea level approximates that of a sector with a radius of 1500 km bounded on the west and east by the land masses of Siberia and Alaska, respectively, and on the south by the Alaska peninsula and Aleutian island arc. Bering Strait is situated near the vertex (Fig. 1). The Sea and Strait are named after Vitus Bering who commanded an extensive Russian expedition during the years 1725 to 1743 which explored the coasts of Kamchatka Peninsula and Alaska.

Bathymetry

The bathymetry is unusual because the neritic (0 to 200 meters) and abyssal (below 1000 meters) zones are about equal in size and constitute almost 90% of the total area. The vast continental shelf extending over 400 miles offshore in the northeastern part of the sea is one of the largest in the world. Continuing northward through the narrow, shallow Bering Strait into the Chukchi Sea, the shelf restricts exchange of all but near-surface water between the Arctic basin and Bering Sea and is sometimes referred to as the Bering-Chukchi platform.

Although the platform is submerged at the present time, geological and paleontological evidence indicates that Siberia and Alaska represent segments of a single continental mass separated by a land connection which has been interrupted by temporary submergence several times during the last 50 or 60 million years. The last submergence is believed to have occurred near the end of the Pliocene or beginning of the Pleistocene epoch, about a million years ago. The continental shelf along the Aleutian island arc and Siberian shore is very narrow. Around the entire Sea, at the edge of the shelf, an abrupt submarine escarpment descends to the floor of the basin. Slopes of 4–5° occur except in the southeastern corner where *Bering Canyon*, perhaps the largest in the world, has a slope of ½°. Two submarine ridges penetrate the basin: *Olyutorski Ridge*, which extends southward from Kamchatka along longitude 170°E almost to the Aleutian island arc and separates the western from the central Aleutian basin, and *North Rat Island Ridge*, which extends northward from the island arc in a counterclockwise direction. The *Alaska peninsula* and *Aleutian island arc*, which restrict the exchange of water between the Bering Sea and North Pacific Ocean, are of late Cenozoic volcanic origin. The island arc, northernmost of a series of arcs in the Pacific, consists of six island groups: Komandorski, Near, Rat, Andreanof, Four Mountains and Fox which rise from depths of approximately 7600 meters in the Aleutian trench and 4000 meters in the Bering Sea basin.

The deepest passage, 4420 meters, occurs at the extreme western end between Kamchatka and the westernmost Komandorski Island. This is also the deepest verified sounding in the Bering Sea. North of this strait a sill at 3589 meters provides the true closure of the basin. Within the deep basin is a vast plain lying at a depth of 3800–3900 meters; a few gently sloping hollows have depths to 4151 meters. Occasional plotted soundings at greater depths are suspect and require verification.

Except for a very narrow passage at longitude 180°, the sill depth eastward of longitude 171°E is considerably less than 1000 meters, and the total cross section permitting exchange of water through the southern boundary is only 731 km^2.

Sediments

Bottom sediments follow a general bathymetric pattern. The continental shelf is covered with sand, near the continental slope the sand changes to silt sizes ("aleurites" of the Russian workers), and the deep basins are covered with clayey diatomaceous oozes. Sediment cores over 30 meters in length obtained from the basins show well preserved shells of contemporary foraminifera and numerous individual lenses of fine and coarse silt and ash material imbedded between layers of ooze. Foraminifera analyses have permitted identification of four horizons which indicate that volcanic activity increased sharply during periods of glaciation, and at the present time the bottom of the Bering Sea has reached its greatest depth since the second half of the Quaternary period.

Climate

The climate of the Bering Sea is not well known because there are no established weatherships or steamship routes that provide periodic observations; practically all climatological data comes from shore stations. Mean air temperatures during winter range from −25°C in Bering Strait to 2°C near the Aleutian Islands, and during summer, the mean temperatures are 6 to 10°C. Precipitation occurs about 35% of the time and snow is common from September to June. Mean sea level pressure varies from 1000 millibars in winter when the Aleutian low is predominant and centered in the southern central part of the sea, to 1011 millibars during summer when the influence of the eastern Pacific high is felt. Although short periods of good weather occur, the sky is usually overcast and fog is frequent.

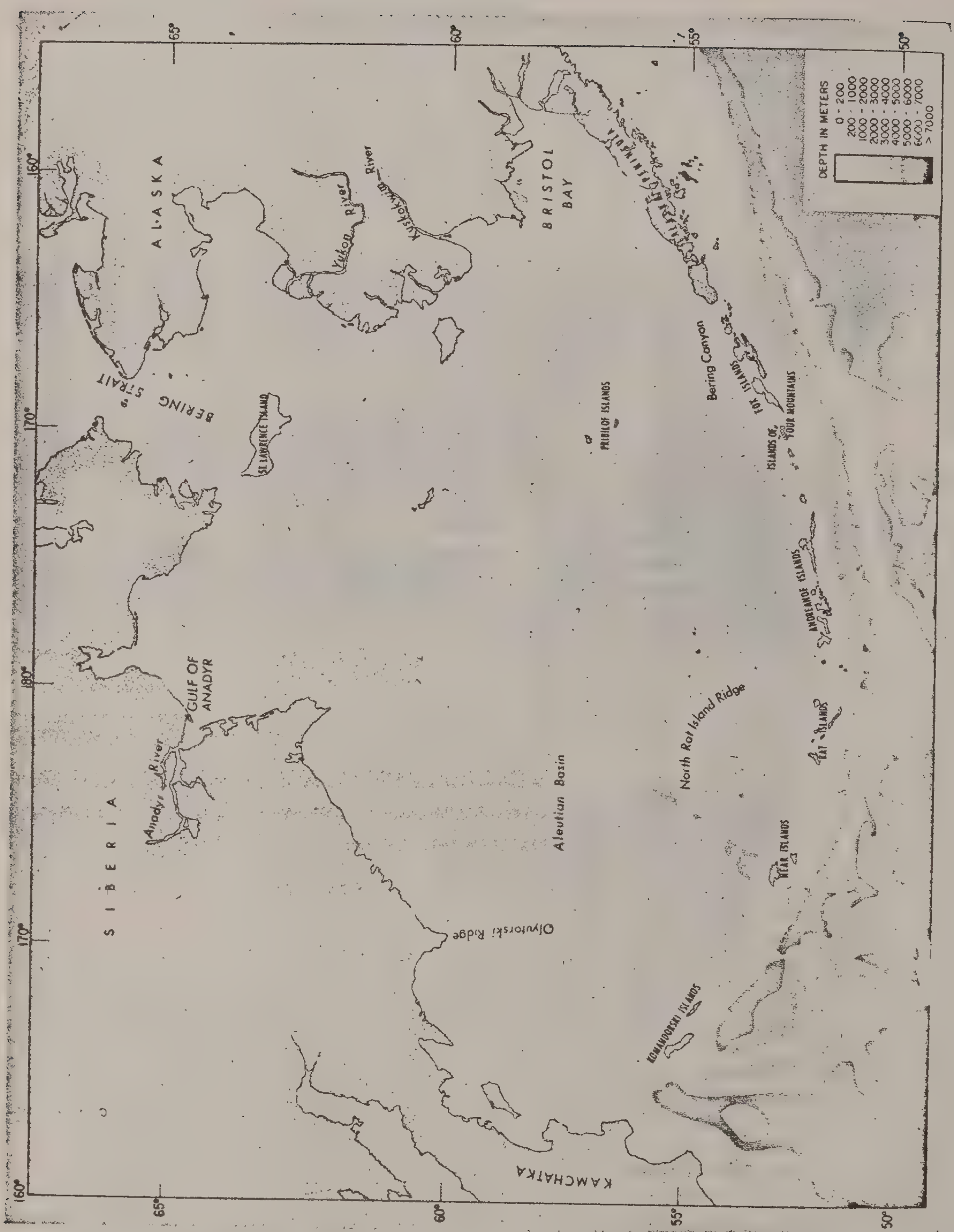
65°
60°
55°
50°
160°
170°
180°
170°
160°
A L A S K A
BRISTOL BAY
Yukon River
Kuskokwim River
ALASKA PENINSULA
BERING STRAIT
ST. LAWRENCE ISLAND
PRIBILOF ISLANDS
Bering Canyon
FOX ISLANDS
ISLANDS OF FOUR MOUNTAINS
ANDREANOF ISLANDS
RAT ISLANDS
NEAR ISLANDS
KOMANDORSKI ISLANDS
North Rat Island Ridge
Aleutian Basin
Olyutorski Ridge
GULF OF ANADYR
Anadyr River
S I B E R I A
KAMCHATKA
DEPTH IN METERS
0 - 200
200 - 1000
1000 - 2000
2000 - 3000
3000 - 4000
4000 - 5000
5000 - 6000
6000 - 7000
> 7000

Fig. 1. Bathymetric map of Bering Sea.

Along the continental coastlines from Kamchatka to Bristol Bay, ice begins to form on the rivers in October and by the beginning of November, fast ice is present in most bays and harbors, and sea ice occurs south of Bering Strait. By January, the sea ice has reached its maximum coverage and extends as far offshore as the 200-meter depth contour. There are two exceptions: off the Kamchatka coast where very cold air moving off the continent permits formation of sea ice

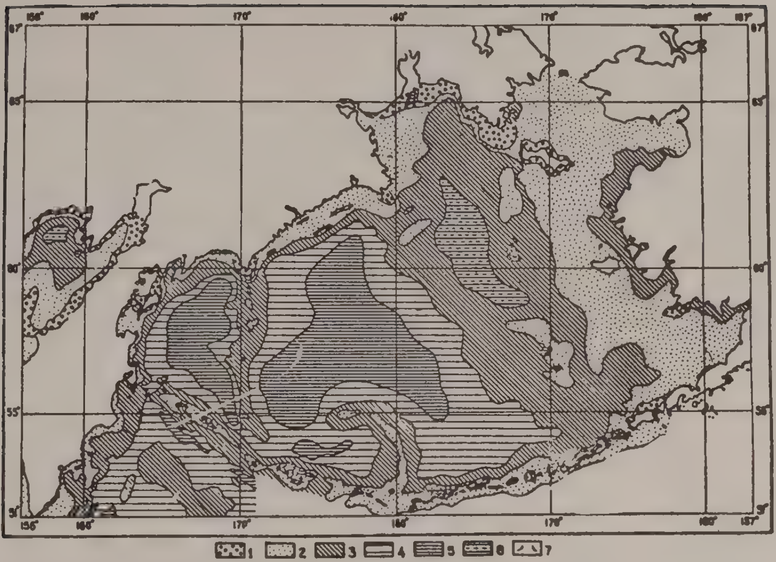

Fig. 2. Sediments of Bering Sea (Lisitzin). 1 Boulders-shingle-gravel; 2 Sands.

well seaward of the 200-meter contour, and along the Aleutian Islands and the western end of the Alaska Peninsula where relatively warm water flowing westward south of the islands inhibits the formation of sea ice anywhere in this area. The sea ice usually covers 80 to 90% of the sea surface indicated, but at no time, even in Bering Strait, is the Bering Sea one solid sheet of ice. Ice flows are usually up to 2 meters thick, and rafting and hummocking, particularly inshore, can result in thicknesses of 5 to 10 meters, but no icebergs are present. The position of the ice field is relatively constant until April, at which time a rapid disintegration and an apparent, northward movement occurs. Ice in the inshore areas, melted by spring runoff, disappears first, and usually by the end of July there is no ice in Bering Sea.

Tides and Currents

Tides along the Siberian coast in the southwestern part of the Sea are diurnal and become mixed at about latitude 60°N; northward of latitude 62°N only semidiurnal tides occur. Along the Alaskan coast from Bering Strait to the Alaska Peninsula mixed tides occur, and diurnal tides are found along the central and western Aleutian Islands. Mean semimonthly tidal ranges are small, 0.5 to 1.5 meters, except in the Gulf of Anadyr and Bristol Bay where they are 2.5 and 5.0 meters, respectively. Tidal currents in some of the Aleutian Island passes have velocities of 150 to 400 cm/sec. Early investigations indicated the Alaskan Stream, which flows westward south of the Aleutian Islands had an appreciable northward component through all island passes, but recent work indicates that the flow in the passes is chiefly tidal with equally strong ebb and flood components. Flow into the Bering Sea which is of basic significance to the water balance occurs at longitude 170°E where the Stream converges with water moving northward in the Western Subarctic Gyre resulting in the formation of a cyclonic eddy over the western Aleutian basin and an anticyclonic eddy in the vicinity of the North Rat Island Ridge (Fig. 3). The main flow continues northward around the Ridge and turns eastward establishing the general cyclonic circulation over the deep basin. In the eastern part of the Sea, cyclonic and anticyclonic eddies are created as the current turns northward adjacent to the continental shelf; and, in the northern part, the current diverges sending one branch northward toward Bering Strait, and the other southwestward along the shores of Kamchatka where it eventually becomes the East Kamchatka Current and discharges back into the North Pacific Ocean. Currents over the continental shelf off the Alaskan coast are chiefly tidal, except adjacent to the coastline where runoff from the Alaskan coast flows northward and is discharged through Bering Strait. Speeds up to 300 cm/sec have been observed near the eastern side of the Strait. The flow is approximately 3 to 4 times greater during August and September than in February and March when ice is present. The principal characteristics of this current, which supplies about 20% of the inflow into the Arctic

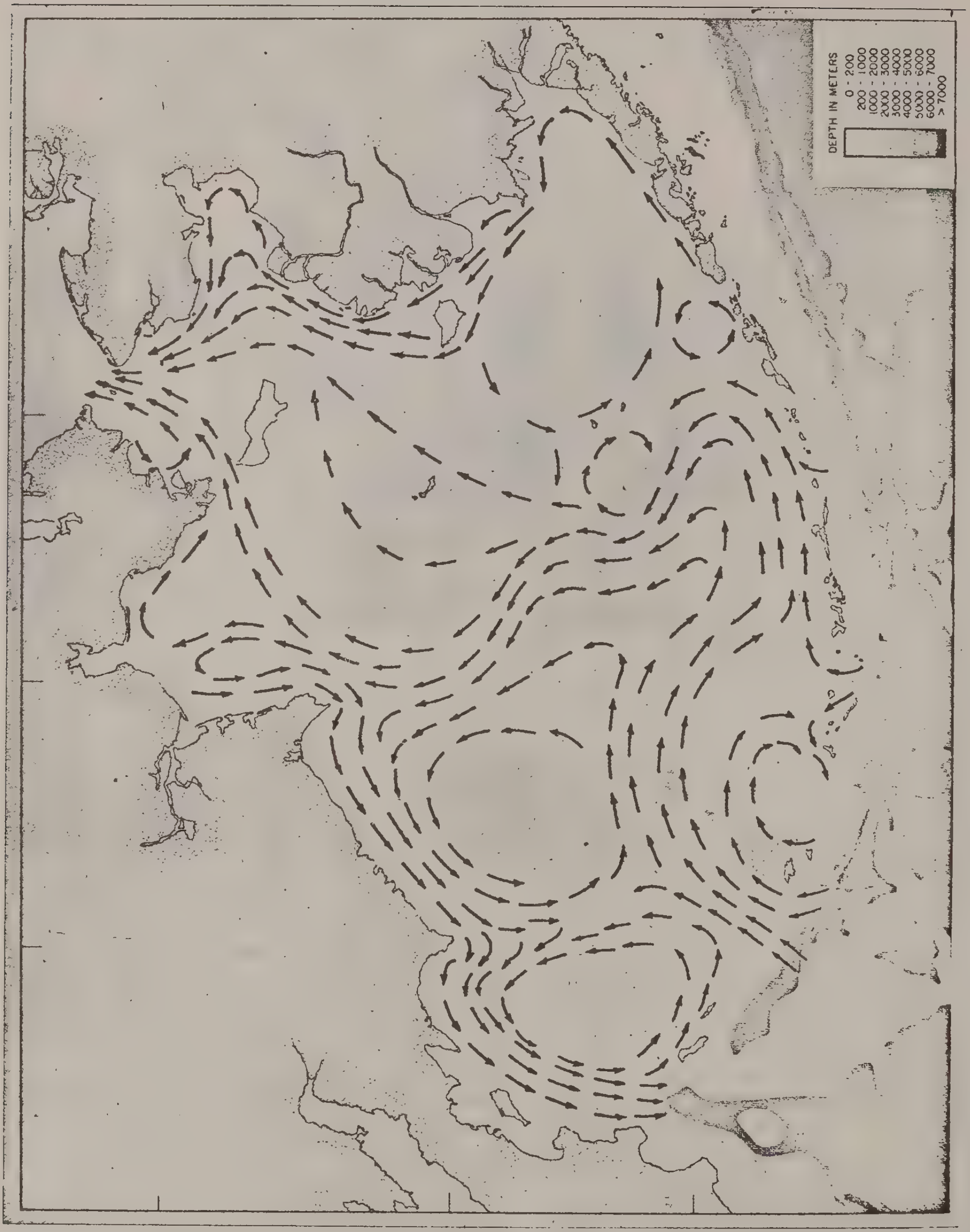
DEPTH IN METERS
0 - 200
200 - 1000
1000 - 2000
2000 - 3000
3000 - 4000
4000 - 5000
5000 - 6000
6000 - 7000
> 7000

Fig. 3. Surface circulation during summer.

basin, can generally be explained in terms of the prevailing winds above the Arctic basin, and Bering and Greenland Seas. In the extreme western part of the Strait, a southward flowing counter current, or "Polar" current, is occasionally observed. Currents at depth are not well known. Although the temperature of the water over the northern shelf is very low during winter, the salinity values are not high enough to permit the formation of deep water. Deep water enters through the passage between Kamchatka and the Komandorski Islands, and is dissipated by a slow, vertical move ment through the weak halocline which exists over the entire basin.

Water Masses

There are three distinct water masses in the Bering Sea. Water over the shallow, broad continental shelf is cooled during winter from the surface to bottom by convection currents under the ice, diluted in spring by runoff from large rivers, such as the Kuskokwim, Yukon and Anadyr, and warmed during summer at the surface. These conditions result in temperatures from −1.6 to 10°C, and surface salinities from 22.0 to 32.8‰ (bottom salinities are slightly higher). Although some low dissolved oxygen values have been reported under the ice, usually near-saturated values are found from the surface to bottom throughout the year. Water in the surface layer (0 to 150 meters) overlying the deep basins originates south of the Aleutian Islands, but is modified by seasonal cooling and heating. Oxygen values are at or near saturation, but, because ice rarely occurs except in the western part, temperatures range from 1 to 9°C and surface salinities are high, 32.9 to 33.2‰. Water below 200 meters in the central basins originates from depths greater than 600 meters in the Pacific Ocean and brings cold, oxygen-depleted water to within 200 meters of the surface (Fig. 4). Separation of water in the surface layer and the water below 200 meters is clearly marked by a temperature-minimum stratum, and a sharp gradient in dissolved oxygen between 100 and 200 meters (Table 1). Temperature and salinity values at the bottom, between 3500 and 4000 meters, are 1.51 ± .02°C and 34.68 ± .02‰.

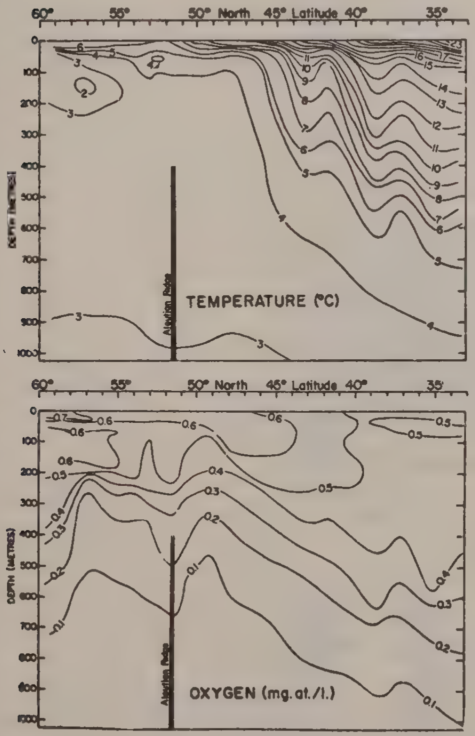

Fig. 4. Vertical sections of salinity, temperature and dissolved oxygen along longitude 180°

TABLE 1. OCEANOGRAPHIC STATION DATA—SUMMER 1962 (LATITUDE 56° 52′ N, LONGITUDE 166° 37′ E)

Depth (m)	Temperature (°C)	Salinity (‰)	O₂ (mg atm/L)
0	10.51	32.94	.620
50	3.02	33.10	.696
100	1.33	33.22	.639
200	3.71	33.88	.104
300	3.60	34.03	.046
500	3.34	34.18	.034
1000	2.63	34.40	.040
2000	1.84	34.59	.120
3000	1.57	34.65	.197
3500	1.53	34.66	.245

Plankton

Although extensive sampling has occurred, the variability in method and period of observation permit only general conclusions concerning the biomass. Of the 163 phytoplankton species reported, 104 are Diatomaceae and 55 Peridinea. The maximum phytoplankton biomass occurs during spring in surface waters over the continental shelf—0.150 to 350 g/m^2 compared to approximately 1.5 g/m^2 in surface waters overlying the deep basin. The biomass decreases in summer, but has a secondary peak in autumn that is about an order of magnitude less than the spring bloom. Vertical distribution studies indicate that the maximum diatom population is not always at the surface and is sometimes found as deep as 30 meters. In late spring and early summer, the number of diatoms vary from 0.3×10^5 to 5×10^8 cells/m^3; the most common forms are *Nitzschia seriata* and *Rhizosolenia hebetata*. Zooplankton, captured in small mesh nets, can be separated into two main groups—oceanic and neritic. In the upper 150 meters of the water column overlying the deep basin, Copepoda represent over 50% of the zooplankton biomass present, the dominant ones being *Eucalanus bungii*, *Oithona similis*, *Calanus plumchrus* and *C. cristatus*; Euphausiacea, chiefly *Thysanoessa longipes* constitute about 25%; Chaetognatha 20%; and Amphipoda, and Pteropoda the remainder. The neritic forms are chiefly Copepoda—*Calanus finmarchicus* and *Acartia* *longiremis*. Very little is known about the vertical migration of zooplankton in this area.

Fish and Mammals

Approximately 315 species of fish are found, of which 25 are of commercial value. The herring, salmon, cod, halibut, ocean perch and flatfish are the most important of the commercial species. King crab and shrimp are commercially important crustacea. Sea otter, sea lion and walrus are found, and the Pribilof and Komandorski islands are nursery grounds for fur seals. Whales such as the killer, sperm, bowhead, humpback, right, finback, sei, beaked and beluga are numerous.

F. Favorite

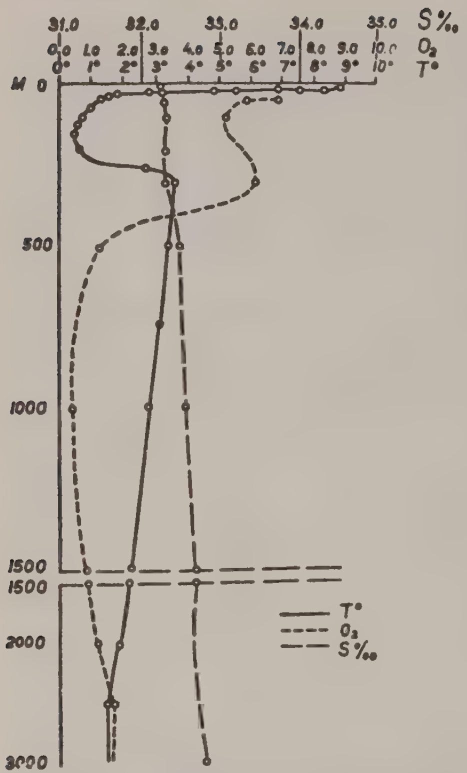

Fig. 5. Vertical distribution of temperature (continuous line), oxygen (short dashes), and salinity.

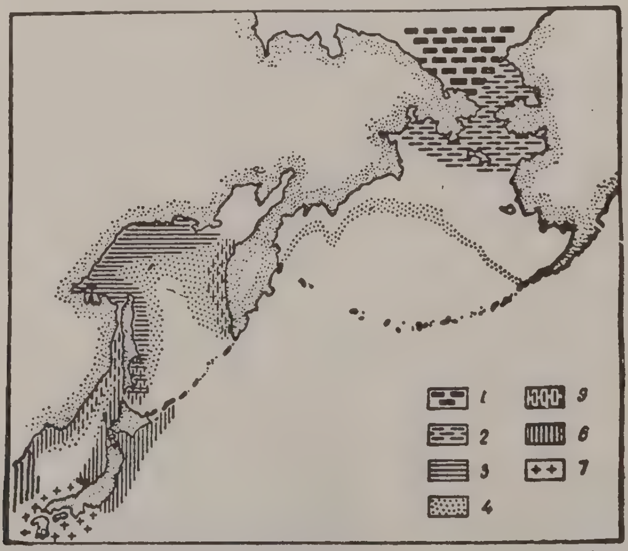

Fig. 6. Zoogeographical regions of the Far Eastern Seas (Vinogradov, 1948). 1 High Arctic; 2 Low Arctic; 3 Glacial; 4 Sub-Arctic; 5 North-boreal; 6 South-boreal; 7 Sub-tropical regions.

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FOOD AND FEEDING BEHAVIOR OF STELLER AND CALIFORNIA SEA LIONS

By Clifford H. Fiscus and Gary A. Baines

Abstract: Sea lions taken on land usually have empty stomachs. To obtain sea lions with food in their stomachs, 34 Steller sea lions and 7 California sea lions were taken at sea. Stomachs of California sea lions contained squids, hake and anchovies. Stomachs of Steller sea lions taken off California and Oregon contained flatfishes and rockfishes; those taken in Alaskan waters contained capelin, sand lance, rockfishes, sculpins, and flatfishes; one had fed on salmon. California sea lions were observed 39 miles and Steller sea lions 85 miles offshore. Large groups feed within 15 miles of land. Farther offshore, sea lions usually occur singly or in small groups of 2 to 12 animals. In summer and early fall, at least, the majority of animals may leave hauling grounds early in the morning and return in late afternoon. No extensive predation on commercial fishes was found. One sea lion contained food amounting to 9.4% of its body weight.

INTRODUCTION

Because sea lions are often numerous, bold and persistent on fishing grounds, they are regarded by fishermen in the North Pacific as the most troublesome animals with which to contend. Interference by sea lions in fishing operations, damage to fishing gear, and destruction of captured fish is often reported. Thorsteinson, Nelson and Lall (1961) summarize damage to the fishing industry by Steller sea lions in Alaskan waters. They state, "The depredations of sea lions in the vicinity of active fisheries are serious because they cause measurable economic losses by damaging fish and gear and intangible economic losses by reducing fishing time or frightening fish away from the gear."

The Marine Mammal Biological Laboratory, Bureau of Commercial Fisheries, has gathered information on the food and feeding behavior of the Steller sea lion (*Eumetopias jubata*) and the California sea lion (*Zalophus californianus*) when they were not competing with an active fishery. These studies were made off the Pacific coast from California to Bering Sea in conjunction with pelagic studies of the northern fur seal (*Callorhinus ursinus*).

RESULTS AND DISCUSSION

Sea lions are difficult to collect at sea. Twenty-three (68%) of 34 sea lions we killed in 1960 sank before they could be recovered; during the same year only 12% of 2,007 fur seals killed were not retrieved. One reason for the greater buoyancy of the fur seal is its dense, water-resistant underfur with entrapped air. Sea lions have no underfur to entrap air and thus are less buoyant.

Because it is difficult to recover sea lions killed at sea, most reports on their food habits have been made from examinations of animals taken on land. Sea lions taken on land are more likely to have empty stomachs or food in advanced stages of digestion than those taken at sea. Several hours may elapse between feeding and hauling out. Mathisen, Baade and Lopp (1962) found that the

TABLE 1.—*Stomach contents of 22 Steller sea lions (*Eumetopias jubata*)*

Age in yrs	Sex	Location and date of capture	Food items	Number	Volume cc	% of total volume
		California				
3	F	18 mi. WSW Pigeon Pt., 3 March 1958	*Citharichthys* sp.	23	1,283	90
			Pleuronichthys sp.	3	142	10
					1,425	
9	F	24 mi. NW Pigeon Pt., 5 March 1959	*Sebastodes diploproa*	5	1,450	84
			rocks	2	275	16
					1,725	
17	F	18 mi. WSW Pigeon Pt., 3 March 1958	*Sebastodes diploproa*	5	1,650	50
			Sebastodes jordani	3	1,320	40
			rock	1	330	10
					3,300	
		Oregon				
6	F	26 mi. W Yaquina Head, 14 April 1961	*Sebastodes* sp.	3	980	100
		Alaska				
1	F	14 mi. E Marmot Cape, Marmot I. 8 May 1960	*Sebastodes* sp.	1	160	30
			Cottidae	3	160	30
			Cyclopteridae	1	108	20
			unidentified fish	1	107	20
					535	
1	F	42 mi. NW Amak I. Bering Sea, 11 July 1960	*Theragra chalcogrammus*	3	840	100
2	M	Unimak Pass, Bering Sea, 13 June 1962	*Mallotus villosus*	1,280	17,560	98
			rocks	6	380	2
					17,940	
2	M	Unimak Pass, Bering Sea, 13 June 1962	*Mallotus villosus*	946	10,670	100
			pebbles	100+		
2	M	Unimak Pass, Bering Sea, 24 Sept. 1962	*Ammodytes hexapterus*	64	565	95
			Mallotus villosus	2		trace
			Pleuronectidae	1	30	5
			Cottidae	1		trace
					595	
2	F	Unimak Pass, Bering Sea, 15 June 1962	*Mallotus villosus*	105	1,370	93
			rocks	15	100	7
					1,470	

TABLE 1. (Continued)

Age in yrs	Sex	Location and date of capture	Food items	Number	Volume cc	% of total volume
2	F	Unimak Pass, Bering Sea, 10 Sept. 1962	*Mallotus villosus*	4	10	17
			pebbles	2	50	83
					60	
3	M	Unimak Pass, Bering Sea, 10 Sept. 1962	Pleuronectidae	1	60	100
3	F	Unimak Pass, Bering Sea, 23 July 1960	Cottidae	7	775	90
			unidentified fish	1	85	10
					860	
4	M	8 mi. E Simeonof I. 4 June 1960	rocks and gravel		310	100
			unidentified fish	1		trace
4	F	Sitka Sound 26 March 1960	*Clupea pallasi*	18	1,425	95
			Atheresthes stomias	1	75	5
					1,500	
4	F	6 mi. NNE Marmot I. 28 May 1960	*Ammodytes hexapterus*	405	2,840	92
			rocks	2	245	8
					3,085	
4	F	Unimak Pass, Bering Sea, 26 June 1962	*Mallotus villosus*	351	2,680	100
			Pleurogrammus monopterygius	1		trace
			Carides	1		trace
			clamshell	1		trace
5	F	2 mi. S Little Koniuji I. in Twelve Fathom Strait 5 June 1960	*Ammodytes hexapterus*	45	290	100
			Heterosomata	1		trace
9	M	6 mi. E. Tonki Cape Afognak I. 23 May 1960	*Mallotus villosus*	27	220	100
9	M	Unimak Pass, Bering Sea, 24 May 1962	*Mallotus villosus*	506	9,605	100
			Ammodytes hexapterus	6		trace
12	F	6 mi. E Tonki Cape Afognak I. 21 May 1960	*Mallotus villosus*	309	2,845	92
			rocks	2	245	8
					3,090	
18	F	39 mi. SW Cape Fairweather 11 May 1958	*Oncorhynchus* sp.	3	3,069	95
			Sebastodes sp.	1	161	5
					3,230	

TABLE 2.—*Stomach contents of six California sea lions (*Zalophus californianus*)*

Age in yrs	Sex	Location and date of capture	Food items	Number	Volume cc	% of total volume
		California				
1+	M	37 mi. WSW Pt. Buchon, 5 Feb. 1959	*Engraulis mordax*	133	2,470	100
	M	Becher's Bay, Santa Rosa I., 18 Mar. 1958	*Loligo opalescens*	59	1,460	100
	M	Becher's Bay, Santa Rosa I., 18 Mar. 1958	*Loligo opalescens* unidentified squid	85 40	1,840 205	90 10
					2,045	
11	M	8 mi. SW San Miguel I. 30 Jan. 1961	*Merluccius productus* unidentified squid rock	18 2 1	5,270	100 trace trace
	F	14 mi. WNW San Miguel I. 19 Mar. 1958	unidentified squid	1		trace
	F	Becher's Bay, Santa Rosa I., 18 Mar. 1958	*Loligo opalescens*	35	1,300	100

stomachs of sea lions just emerging from the water contained no more food than those already on land.

From 1958 to 1963 we took 34 Steller sea lions and 7 California sea lions at sea. The stomachs of 22 of the Steller sea lions and 6 of the California sea lions contained food. Because there is almost no published information on stomach capacity or variety of food in individual stomachs, the data are presented separately for each animal (Table 1–2). Since volume (cubic centimeters) of food and weight (grams) of food are nearly equal, weight is omitted from these tables.

Analysis of stomach contents based on occurrence only, without consideration of volume, is misleading, particularly regarding animals taken on hauling grounds or rookeries. Otoliths and characteristic bones of medium-sized fish persist in the stomach longer than otoliths and bones of small fish. Large fish bones and squid beaks remain in stomachs long after soft parts are digested and may persist over several feedings on small, fragile species. Collections made at sea where sea lions are feeding give better estimates of maximum food consumption and of the relationship of food intake to body weight.

Records of stomach contents (Table 1–2) show that the food species vary from one area to another. Variation of food species according to depth of water and length of time that a food species is available in a particular locality are not easily shown. The California sea lions taken off southern California had eaten mainly squids and small, schooling fishes. Steller sea lions taken off central California and Oregon had fed only on bottom fish. The Steller sea lions taken in Alaskan waters had fed mainly on small, schooling fishes. Near Unimak Pass in 1962, capelin (*Mallotus villosus*) was the major food species. A Steller sea lion taken on the Fairweather Grounds in the eastern Gulf of Alaska in May 1958 had eaten three salmon (*Oncorhynchus* spp.).

Most of the food species (capelin, sand lance, sculpins, rockfishes and flatfishes) found in the stomachs of Steller sea lions suggest that they feed near land or in relatively shallow water (< 100 fm, 180 m). The food species (squids, anchovy and hake) taken by California sea lions are found in both shallow (< 100 fm, 180 m) and deep (> 100 fm, 180 m) water. Sea lions were taken while we were hunting for fur seals, a truly pelagic species. Therefore a greater dependence on pelagic food may be indicated in our sample than would be shown by a sample from a greater range of feeding habitat.

We also found stones up to 12 cm in diameter in 7 of 12 otherwise empty stomachs and 9 of 22 stomachs with food. Why stones are swallowed is not known, but the fact that seals and sea lions do this is well documented in the literature.

Both species of sea lions may travel considerable distances from their rookeries or hauling grounds to feed. We found, however, that the Steller sea lion occurred at greater distances from land than the California sea lion. The greatest distance from land that we saw California sea lions was one sighted in lat. 34° 53′ N, long. 121° 34′ W, about 39 miles SW of Point Buchon, California, 1 February 1959. Steller sea lions were seen at distances of 70 and 85 miles from land by Fiscus and Kenyon in 1960 (Kenyon and Rice, 1961).

We saw Steller sea lions at many localities in the northern Gulf of Alaska in April and May, 1958 and 1960. During July and August 1963 we found them throughout the eastern Bering Sea between the Pribilof Islands and the Aleutian Islands. We seldom found large groups of sea lions (100 or more) feeding more than 10–15 miles from a hauling ground or rookery, but we found small groups (2–12) and individuals far from the nearest land.

During late June and July 1960 and from May to October 1962 we observed feeding behavior and collected Steller sea lions in the vicinity of Unimak Pass, Alaska. In general during these months the sea lions left their hauling grounds in early morning, in compact groups of several hundred to several thousand animals. They then swam 5 to 15 miles out into feeding areas in or adjacent to Unimak Pass. There they dispersed into smaller groups of less than 50 animals. The feeding groups usually contained both sexes and mixed sizes of animals. In the late afternoon they again formed into large groups and returned to the hauling grounds.

The massing described above occurred where sea lions were feeding on schooling fishes or squids. Where large schools of prey were absent, sea lions fed singly or in small groups of two to five animals. Similar behavior was observed for Steller sea lions in other parts of Alaska and for California sea lions off San Miguel Island, California.

One 2-year-old male Steller sea lion which weighed 191 kg was shot while feeding. The stomach appeared to be filled to near maximum capacity and contained 1,280 capelin weighing 18,050 g. The food consumed amounted to 9.4% of the animal's total body weight.

Estimates of the annual food intake of sea lions cannot be made on the basis of present knowledge. Further information is needed on the frequency of feeding; the differences in food requirements according to body size, age, sex and season; the effect of fasting behavior of males on feeding activity during the breeding season and the influence of weather and migratory fish populations on feeding activity.

Our data indicate that sea lions may not prey extensively on free swimming salmon or other fishes that are important to commercial fishermen. This is the general conclusion indicated by the reports of other investigators (Imler and Sarber, 1947; Pike, 1958; Thorsteinson and Lensink, 1962; Mathisen, Baade and Lopp, 1962). More comprehensive studies are necessary before it is possible to assess the degree to which sea lions feed on commercially important fishes and the amount of damage they inflict on commercial fishing gear.

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INSTRUCTIONS FOR COLLECTING BLOOD AND SERUM SAMPLES FROM TUNA FISHES

by

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FOOD AND AGRICULTURE ORGANIZATION OF THE UNITED NATIONS
Rome, February 1966

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Certain characteristics of blood in fish, as in other animals, follow the Mendelian laws of inheritance and are little affected by the environment throughout the life of the animals; included are blood groups and inherited differences in serum components that can be detected with immunological or biochemical techniques (Cushing, 1964; Fujino, 1960; Marr and Sprague, 1963; Parrish, 1964). These characteristics thus are potential "genetic markers" of intraspecific, isolated, breeding populations, called "subpopulations", "unit stocks", or "races". The delineation of such subpopulations is most desirable for effective management of fishery resources.

In recognition of the importance of population genetics in the study of tuna, a recommendation was made at the 1962 World Scientific Meeting on the Biology of Tunas and Related Species "that there be established a Tuna Blood Group Center to promote the exchange of tuna erythrocytes, reagents for the typing of tuna bloods, and information on tuna blood group research and that the Bureau of Commercial Fisheries Biological Laboratory at Honolulu continue to act in that capacity" (Rosa, 1963). The Tuna Blood Group Center in Honolulu had been established in 1960 to conduct research on fish genetics.

The FAO Expert Panel for the Facilitation of Tuna Research (1964) called attention to "the need for a standardized set of collecting instructions for blood and serum specimens." It requested that the Tuna Blood Group Center prepare such instructions. The present circular was prepared to satisfy the request, and to make available in essentially outline form the techniques used at the Tuna Blood Group Center for the collection of samples of blood and serum from tuna fishes.

Those who wish more detailed instructions or who wish to cooperate in obtaining samples for analysis at the Tuna Blood Group Center should write to the Director, U.S. Bureau of Commercial Fisheries, Hawaii Area, Honolulu, Hawaii 96812.

MATERIALS NECESSARY FOR COLLECTING SAMPLES

1. Ten- or 50-ml plastic or glass tubes for samples. The larger tubes are preferable, especially for samples of whole blood from new geographic areas.

2. Plastic hypodermic syringes, and needles.

3. Data forms (fig. 1).

4. Dry ice or plastic bottles filled with ice.

5. Thermos (vacuum bottle) or container made of insulating material.

6. Glycerol solution for preservation of erythrocytes by freezing. This solution consists of 6 parts of water containing 5 percent trisodium citrate, and 4 parts of glycerol. A few milligrams of additional antimicrobic or antibiotic, such as triple sulfa (which contains sulfathiazole, sulfadiazine, and sulfamerazine),

DATA SHEET FOR BLOOD SAMPLING KITS

Vial number	Species	Date caught	Area caught	Size forklength or pound	Sex	Remarks

Figure 1. Form used by Tuna Blood Group Center for recording data taken in conjunction with samples of blood and serum

guanofuracin (5-Nitro-2-furfurylidine-amino-guanidine hydrochloride), or streptomycin are recommended to prevent deterioration due to accidental warming during preservation and transportation.

7. Freezer at a temperature of -15° C or lower for preserving samples.

8. Centrifuge with a speed of about 1,000 r.p.m., for separating serum from whole blood.

TAKING BLOOD FROM FISH

The three principal methods of collecting samples of fish blood follow. Use only the fresh fish as the source.

1. Fit the syringe with a needle; plung the needle into the isthmus between the opercula, in line with the back of the opercula (fig. 2). Apply a steady negative (withdrawing) pressure to the plunger. When blood appears in the chamber of the syringe, the heart or conus has been reached and the sample can be taken. Some movement of the needle may be necessary to prevent clogging and permit the maximum amount of blood to be sampled.

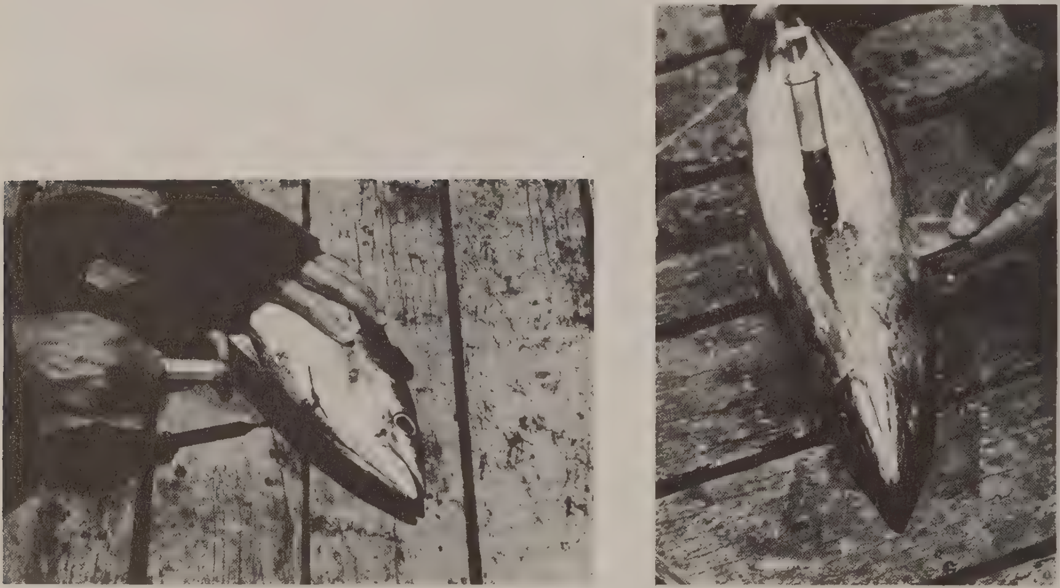

Figure 2. To withdraw blood from a tuna, insert needle into isthmus between opercula, in line with back of opercula. Photographs show operation from different angles

2. Insert the needle through the opercular opening, lifting the gills to obtain clear access. For best results, aim the needle at a very oblique angle, in a distinctly caudal direction. Some probing dorsally or ventrally may be necessary. Steady negative pressure on the plunger will draw blood into the chamber of the syringe when the heart or conus is reached.

   A variation of this method is to plunge the needle into the fish without the syringe attached and bleed directly into the collecting vial or a clean beaker. This procedure is effective only when the fish is still alive.

3. A third method (which is recommended only if the fish weighs more than 5 k, and if the other methods have failed) is to completely sever the tail and allow the blood to flow into a clean jar or beaker from the dorsal vein. This method is less satisfactory than the first two, because the possibility of contamination

is increased. Great care must be exercised when drawing blood, to keep fish slime, stomach juices, perspiration, dirt, or grease out of the syringe or collecting vial. Such foreign substances ruin the sample.

Only 0.5 ml of blood and serum is required for routine tests, but initial studies require larger volumes from each fish sampled.

PRESERVATION OF BLOOD CELLS

After drawing the blood into the syringe, express it into a vial containing the glycerol solution. A given volume of this solution preserves up to an equal volume of blood. Leave space at the top of the vial equal to about one-tenth of its capacity, to allow expansion during freezing. After taking each sample, immediately rinse the syringe and needle in fresh, clean sea water to prevent contamination from one sample to the next.

As soon as possible, the vials containing the samples should be placed in a freezer and kept at -15° C or below, until the samples are analyzed. If freezing facilities are not available at the time of collection, the specimens can be kept in good condition for a few days by refrigeration, prior to freezing.

The blood cells can be recovered by dialyzing blood samples against isotonic saline through a cellophane tube for 2 hours or so at room temperature and by successive washing. (Cushing, Ridgway and Durall, 1957; Suzuki, Shimizu and Morio, 1958; Cushing, Fujino and Takahashi, 1959).

SEPARATION AND PRESERVATION OF SERUM

After taking blood by the techniques described above, express it into a clean dry test tube and allow it to form a clot; then centrifuge at about 1,000 r.p.m. for 5 minutes to separate the serum. The clotting and centrifugation should be performed in a shaded area, to reduce hemolysis and contamination of the serum with hemoglobin. Slight hemolysis is permissible, but serum samples of wine color or darker (caused by heavy hemolysis) cannot be used for analysis. Pipette the serum to a vial (use a clean test tube and pipette for each sample, to prevent contamination from one sample to the next), and preserve it in the freezer at -10° C or below. To avoid changes in pH and other factors which might affect the samples, do not add preservative.

RECORDING DATA

Number the vials and keep a record on the appropriate form (fig. 1); indicate vial number, species, date caught, area caught, size and sex.

TRANSPORTATION OF SAMPLES

When air transportation is available, DIRECT SHIPMENT BY AIR FREIGHT is best, though airmail special delivery may be used if commercial airlines will not accept the container as cargo.

Samples must be refrigerated with dry ice or ice while in transit. If dry ice (highly recommended) is not available, use plastic bottles that have been filled with water and kept in a freezer until the water is solidly frozen. Delay packing the container until close to plane-departure time. If facilities for refrigerating or freezing are available at the airport, use them.

The laboratory receiving the samples should be informed in advance by telegram of the name of the airline, the flight number, and the date and time of arrival.

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Vertebral Abnormalities in Sockeye, Pink, and Chum Salmon

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ABSTRACT

Radiographs of vertebral structures of 10,377 sockeye, 4,403 chum, and 4,777 pink salmon collected in 1958 to 1962 were examined to determine the frequency of occurrence of abnormal vertebrae in wild populations of mature Pacific salmon. Various types of deviations from the orderly processes of development or segmentation that resulted in abnormal structures were classified as fusions or abnormalities. The frequency of occurrence of abnormalities in the vertebral column was tabulated by species, sampling locations, and year of sampling. Abnormalities were found in the vertebral columns of 2.8% of the sockeye, 3.3% of the pink, and 2.9% of the chum salmon. Differences in frequency of occurrence of abnormalities among the species were not statistically significant. In sockeye salmon, 47% of the abnormalities were in the caudal region and 42% in the abdominal region; in pink salmon, 39% were in the caudal and 49% in the abdominal region.

INTRODUCTION

In racial studies on Pacific salmon by the Bureau of Commercial Fisheries, morphological characters were examined as a means of distinguishing salmon populations on the high seas (Fukuhara et al., 1962). To examine these morphological characters, counts of various meristic characters were made from a large number of sockeye salmon (*Oncorhynchus nerka*), pink salmon (*O. gorbuscha*), and chum salmon (*O. keta*). To aid in making these counts all specimens were radiographed. These radiographs provided us with a unique opportunity to study vertebral abnormalities in the three species and to determine whether the frequency of abnormalities differs in different parts of the vertebral column.

Vertebral abnormalities apparently are rather frequent in many species of fish, but the types and frequencies of abnormalities have been studied comprehensively for only a few species. Furthermore, the relative roles of genetic and environmental factors have not been closely defined.

Ford and Bull (1926) described five classes of vertebral fusions in herring. Gabriel (1944) presented information on types of abnormal vertebral development and frequency of fusions observed during an experimental study of *Fundulus*; he discussed in detail some possible causes of the abnormalities. Gabriel observed that a certain type of vertebral abnormality was caused by high temperatures during embryological development. Seymour (1959) studied the effect of temperature on vertebral development in chinook salmon (*O. tshawytscha*) hatched in the laboratory and concluded that the high frequency of fusions was correlated with both high and low temperatures while the embryos were developing.

The radiographs from the racial studies on sockeye, pink, and chum salmon were examined for abnormalities to determine: (1) the anatomical details of abnormalities in the vertebrae and attached elements; (2) their frequency of occurrence by species and geographical area; and (3) their comparative frequency in different vertebral regions.

PROCEDURES

Data for this study are principally from vertebral radiographs of North American salmon collected in 1958 to 1962 in streams and estuaries from Washington to Alaska. Some data are from samples received from Japanese land-based fisheries. One sample of sockeye salmon and two of chum salmon were collected from Russian land-based fisheries in 1959. Details of sampling sites, numbers of specimens, and percentage of abnormalities are available from the authors.

In the laboratory the frozen specimens were thawed and eviscerated in preparation for radiographing. A probe was used to locate the first complete bony hemal arch. A $\frac{3}{4}$-inch length of lead wire was attached to the arch for identification in the radiographs. This procedure, which provided accurate identification of the first arch on the radiographs of sockeye and pink salmon, enabled us to define the abdominal and caudal regions of the vertebral column and to tabulate separately the

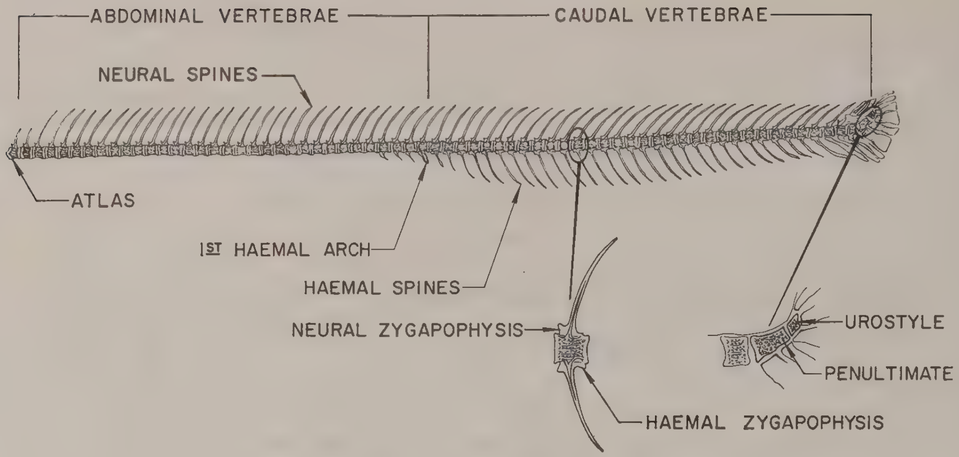

FIGURE 1.—Sockeye vertebral column showing various structures.

abnormalities in each. The abdominal region of the vertebral column was defined to include the atlas and all other vertebrae anterior to the first hemal arch; the caudal region included the portion extending from the first hemal arch to the most posterior vertebra (Figure 1). The term "central region" was used as an aid in making an accurate count of abnormalities where fused vertebrae obscured the division between abdominal and caudal regions.

In chum salmon, identification of the first hemal arch was inaccurate because of the variability in its degree of ossification; "firmness" of the "completed" arches gradually increased posteriorly, so that it was difficult to decide which was the first hemal arch, and which was only "bridged" by tissue. In addition, the tissue was often broken in handling. Consequently, the first hemal arch of chum salmon could not be designated on the radiographs as a reference point for identifying the region of the vertebral column in which abnormalities were located.

The percentages of sockeye, pink, and chum salmon with abnormal vertebrae were calculated for each sample, and for major geographical areas. For sockeye and pink salmon, the percentages of abnormalities within each vertebral region were also calculated, by sample and major geographical area. The abnormalities tabulated were those which appeared to cast some doubt on the taxonomic usefulness of vertebral counts.

TYPES OF VERTEBRAL ABNORMALITIES

The various types of deviations from the orderly processes of development or segmentation that resulted in abnormal structures were classified as fusions or abnormalities. These types are illustrated in Figures 2 to 10, and a composite of different types were sketched from dissected specimens (Figure 11).

Adjacent vertebrae that lacked distinct intervertebral separation were classified as abnormalities. Some abnormal vertebrae differed in shape and size from adjacent normal vertebrae; others, though not irregular in shape and size, had duplicated neural or hemal arch elements, or both. Prominent duplications of the neural arch elements (Figure 2) were tabulated as abnormalities. Vertebrae with less prominent duplications, such as the bifurcated neural arch elements shown in Figure 4 (apparently the result of the failure of the lateral arch elements to join properly to form the neural arches, without influencing the vertebrae), were not recorded as abnormalities.

Figures 2 to 10 are radiographs of the various types of abnormal vertebrae which were tabulated. The captions indicate the location of the abnormality within the verte-

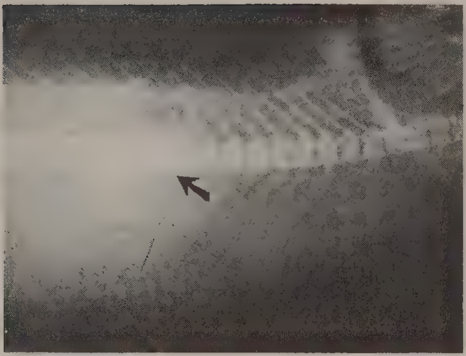

FIGURE 2.—Fusion of two vertebrae with three pairs of neural and hemal arch elements on the posterior centrum in the complex.

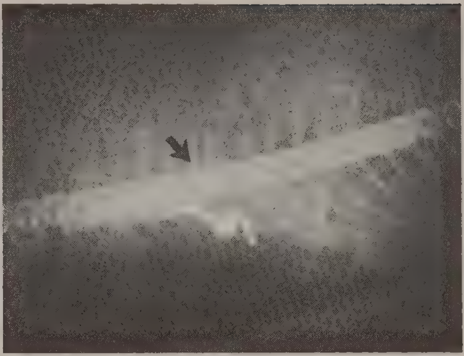

FIGURE 4.—Abnormal vertebrae in the region of the first hemal arch. One abdominal and two caudal vertebrae are involved in the complex.

bral column. Each of the structural abnormalities occurred in all three species of salmon.

Some of the structural aberrancies included as abnormalities in the data did not necessarily affect the accuracy of counts of the centra.

FREQUENCY OF VERTEBRAL ABNORMALITIES

Frequency of occurrence of abnormalities in the vertebral column was tabulated by species, sampling locations, and year.

Sockeye salmon

Radiographs of 10,377 sockeye salmon from 59 samples collected in different localities or years were examined. As many as 9.6% of the specimens in different samples had vertebral abnormalities; the average (all abnormalities combined) was 2.8%. The greatest percentage of specimens with abnormalities (9.6) was in a sample of 125 fish (12 with fused vertebrae) collected in the Copper River in 1959. The large number of samples from the Bristol Bay area provided a good measure of variability within an area. The percentage of specimens from Bristol Bay that had vertebral abnormalities varies from 0.5 to 7.5 in different years or tributaries; the highest percentage was in Wood River in 1961 (15 abnormalities in 200 fish).

The distribution of the abnormalities within the vertebral column, calculated as the percentages in the abdominal, central, and caudal regions, for each major geographical area, also varies widely. Vertebral abnormalities in 296 sockeye salmon (from all geographical

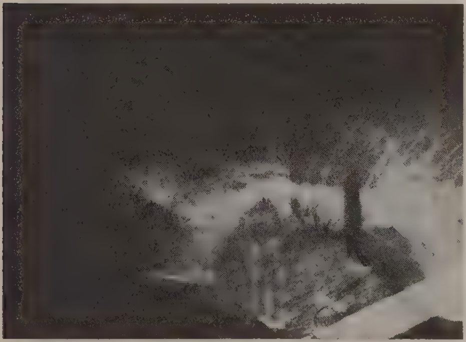

FIGURE 3.—Abnormally small vertebrae.

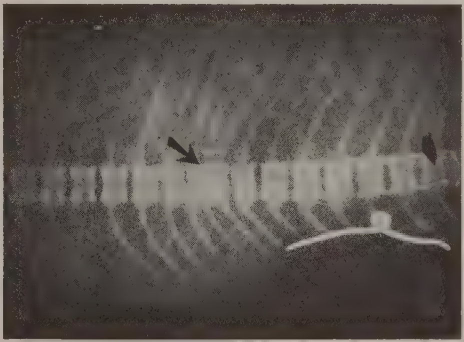

FIGURE 5.—A fusion of three abdominal vertebrae.

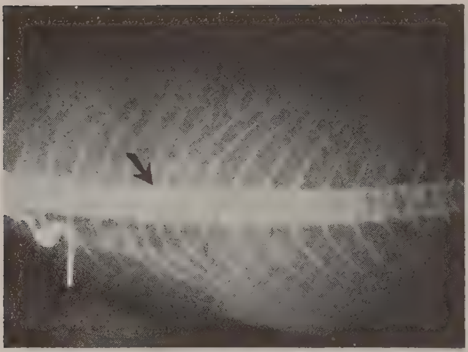

FIGURE 6.—A fusion of three caudal vertebrae.

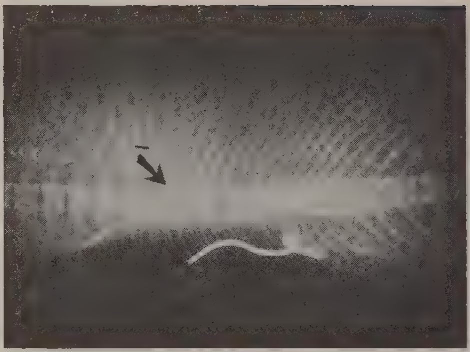

FIGURE 8.—A mass fusion in the central region of the vertebral column involving both abdominal and caudal vertebrae.

areas combined) were located in the abdominal region in 42% (125 fish), in the central region in 10% (31 fish), and in the caudal region in 47% (140 fish). The percentages of abnormalities in the major vertebral regions were reversed for samples from the tributaries of Bristol Bay considered separately—48% were in the abdominal region and 42% in the caudal.

In some collections, deviations from the average percentages were large (e.g., in the sample from the Ozernaya River, in which three or four abnormalities were in the abdominal region), but the total number of deformed fish was small.

Pink salmon

Of 4,777 pink salmon in 47 samples, 3.3% had vertebral fusions. This percentage did not differ statistically from that for sockeye salmon. Values for individual samples ranged from 0 to 10.7%. The average percentages of abnormalities in samples from southeastern Alaska and British Columbia were 4.1 and 4.9, both above the species average.

A total of 158 pink salmon had vertebral abnormalities; 48.7% were in the abdominal region, 12.7% in the central region, and 38.6% in the caudal region. The location of fusions varied considerably among the individual samples; of 13 abnormalities in 376

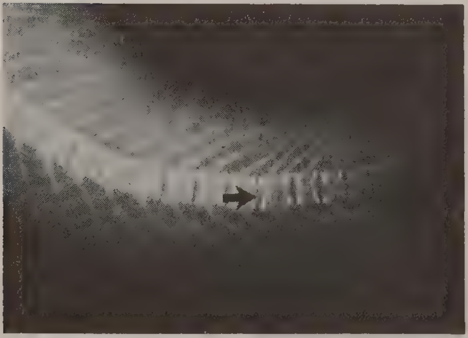

FIGURE 7.—Fusion of the seventh and eighth vertebrae from the posterior end of the vertebral column.

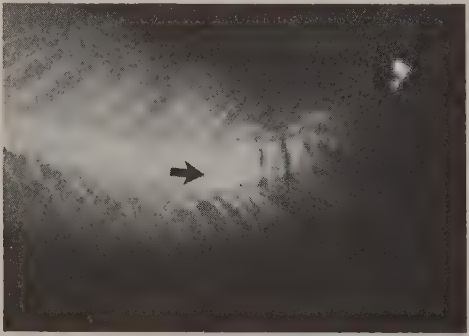

FIGURE 9.—Distortion of vertebrae in the posterior caudal region.

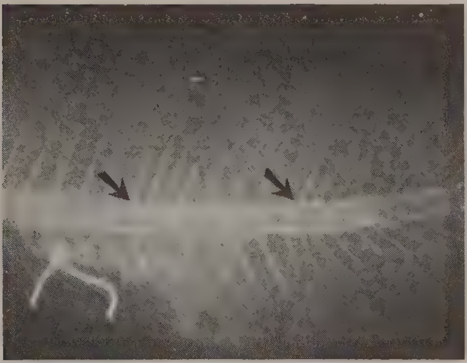

FIGURE 10.—Two occurrences of fusion of vertebrae in the caudal region.

salmon from the Japanese land-based fisheries, about 69% were in the caudal region and 31% in the abdominal region.

Chum salmon

In 4,403 chum salmon in 48 samples, the percentage with abnormal vertebrae was 2.9; the range among the samples was 0 to 8.7. Among the different geographic areas, samples from Kodiak Island had the highest average (5.8%), followed by samples from the Kamchatka Peninsula (4.5%). The frequency of occurrence of vertebral abnormalities in chum salmon did not differ significantly from that in pink salmon or sockeye salmon.

RELATION OF VERTEBRAL ABNORMALITIES TO TAXONOMIC STUDIES

The percentage of abnormalities found in 19,557 sockeye, pink, and chum salmon was about 3.0. The frequency of occurrence of abnormalities corresponded closely to the 2 to 3% in wild populations of *Fundulus* discussed by Gabriel (1944). He suggested that the higher percentage (30.0) found in laboratory specimens could have been induced by some general physiological depressor under experimental conditions. A further possibility is that he may have observed fused vertebrae in fish that would not have survived to adulthood, because of vulnerability related to the abnormal development.

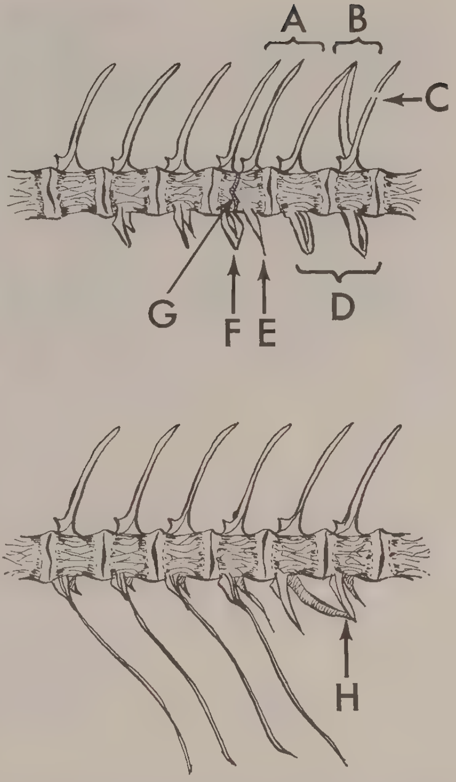

FIGURE 11.—Various types of vertebral abnormalities. A. Two neural arch elements on one vertebra. B. Left neural process of anterior vertebra in junction with one right process from the succeeding vertebra. C. Abnormal neural arch and spine. D. Normal haemal arches. E. Extra left haemal process only. F. First haemal arch. G. Suture on left side only—not apparent on right side. H. Arch completed with right process of one vertebra joining left process of the succeeding vertebra.

A chi-square test showed that this difference was not significant. Gabriel (1944) and Seymour (1959) found that *Fundulus* and chinook salmon, respectively, had abnormalities more frequently in the caudal region. Of the vertebral abnormalities in sockeye salmon, approximately 42% were in the abdominal region of the vertebral column and 47% in the caudal region. The remaining 10% were in the central region and included both abdominal and caudal vertebrae. In pink salmon, 49% of the abnormalities were in the abdominal region, 39% in the caudal region, and 13% in the central region.

Conclusive evidence on the roles of genetic and environmental factors on vertebral abnormalities in salmon and other fish will require controlled laboratory experiments and correlated field studies that include the observation of the developing fish in different environments, from the egg through various life history stages. These experiments may be warranted since much interest in abnormal conditions generally arises when reliable vertebral characters are sought. It seems likely, however, that the incidence of fusions or other major abnormalities in wild populations is too low in adult fish, and possibly in larval stages, to be of serious consequence in taxonomic or racial studies if specimens with abnormal vertebrae are merely eliminated.

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Order Iniomi[1]

COMPOSITE AUTHORSHIP

Characters and Synopsis of Families

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Characters. The same as those in the Order Isospondyli in most respects, but differing in the exclusion of the maxillary from the gape by the premaxillary; in the type of association between the anterior end of the palatine, the proximal end of the maxillary, and the lateral projection of the ethmoid; in the absence of a mesocoracoid arch in the pectoral girdle; in the absence of the transverse ethmoidal commissure connecting the sensory canals along the sides of the skull roof; and in the fusion of the innermost pterygiophore of the pelvic fin with the innermost pelvic ray; but no single one of

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[1] The Order Iniomi (Scopeliformes of Berg) as used here excludes several groups that have occasionally been included: the Giganturidae (Part 4, p. 570); Cetomimidae; Rondeletiidae and Barbourisiidae, accounts of which will appear in a later volume; Ateleopidae and Miripinnati, which also will appear later; *Bathylaco* (Part 4, p. 562); and *Macristium*, an extralimital monotypic genus of uncertain affinities (see Regan, *22*).

Gosline has considered the osteological distinctions between the Iniomi and the Isospondyli and has suggested the myctophoid groups. His work was made possible by a Guggenheim Fellowship and was accomplished in the United States National Museum. He is indebted to Leonard P. Schultz and the staff of the Division of Fishes for space and equipment in that institution, to Giles W. Mead and Daniel M. Cohen of the U. S. Fish and Wildlife Service for background information, specimens, and literature, and to N. B. Marshall for his many valuable comments and suggestions. Marshall has written the alepisaurid introduction. Mead has provided the portions regarding the Iniomi as a whole.

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these features is diagnostic; each is subject to qualification.[2] Under these circumstances, it seems advisable to include here a discussion of these characters and the relationships of the Iniomi.

Discussion.[3] To many ichthyologists, the fishes considered here as representatives of the Order Iniomi are sufficiently similar to those of the preceding Order, Isospondyli, to be included within that group.[4] Certainly many of the features characteristic of the isospondylous fishes (Part 3, pp. 89–106) are duplicated in iniomous species. Among these are the nature of the fins and fin rays, including the degree of branching, the lack of true spines, the frequent presence of an adipose fin, the high number of branched caudal rays (typically 17), and the frequent posterior (abdominal) position of the ventral (pelvic) fins. Similar, too, are the various patterns of scale coverings, the nature of the individual scales, and the development of photophores in certain groups of both Orders.

Other features are more nearly diagnostic for the iniomous fishes. Thus the invariable absence of a mesocoracoid arch in the pectoral girdle and the closed swim bladder (when present) are duplicated in only a few isospondylous forms.[5]

The ethmoid-palatine-maxillary series of articulations also belong in the same category. In most iniomous fishes, as Regan noted (*23*), the anterior end of the palatine (Fig. 1) forms "a process directed upwards and outwards which overlaps the proximal end of the maxillary and is supported by a lateral projection of the ethmoid." The portion of the maxillary over which this palatine process projects is not only far forward but consists of a flat area or depression, with at most a very slightly raised articular socket, on the upper maxillary surface. In the isospondylous fishes there is considerable variation in the nature of the palatine-maxillary articulation (*cf.* Fig. 1 A, B). Most frequently, perhaps, the palatine has a sort of elbow that overlaps a nodule on the dorsomedial surface of the maxillary, as in Fig. 1 B; this nodule is lateral to, and well separated from, the anterior maxillary head.

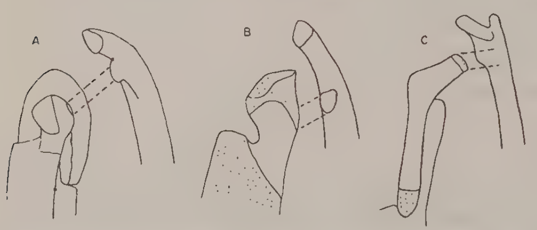

FIGURE 1. Right palatine-maxillary articulation in A, *Tarpon*, B, *Yarrella*, and C, *Chlorophthalmus*, from above. The maxillary has been pulled away from the palatines, the pair of dashed lines indicating the articulating areas of the two bones concerned. Stippling indicates cartilage.

Unfortunately, this differentiation does not always hold for all the members of either the Iniomi or the Isospondyli. Among the latter, some of the southern hemisphere representatives, *e.g. Galaxias* and *Aplochiton*, have a palatine-maxillary articulation much like that just described for the Iniomi. There are also iniomous fishes without such a palatine structure. Thus, among the alepisauroid inioms, *Evermannella* has the palatine-maxillary articulation typical for the Order; *Alepisaurus*, *Omosudis*, and *Sudis* have it in modified form; but *Lestidium* appears to have no articulation whatever between the anterolateral palatine projection and the maxillary. Also, among certain myctophoid inioms, such as *Harpadon* and *Bathysaurus*, the maxillary has either dropped out or has become fused to the premaxillary so that the palatine head appears to articulate directly with the premaxillary.

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[2] Bigelow (Part 3, p. 92) has noted the withdrawal of the maxillary bone from the border of the gape in several typical clupeoid and elopoid isospondyls: *Chaetoessus*, *Albula*, and *Pterothrissus*.

[3] For further information on the anatomy and major classification of the iniomous fishes, the reader is referred to Regan (*23*), Parr (*19*; *20*), and Marshall (*14*).

[4] For example, Schultz and Stern (*24*) and Bertin and Arambourg (*2*).

[5] Among isospondylous fishes the mesocoracoid arch is lacking only in the haplomous fishes and certain salmonoid and stomiatoid forms; the swim bladder is closed only in the stomiatoids and certain deep-sea salmonoids (*11*).

The chief character usually used to separate the Iniomi from the Isospondyli is the difference in premaxillary construction. Chapman (*4*) has summarized the problems involved in this mode of separation as follows:

> . . . the Isospondyli and Iniomi as recognized by Regan and Jordan (and generally by present day ichthyologists) have only one distinguishing characteristic which all members of each order share, and that is that in the Iniomi all members have the maxillary excluded from the gape by the premaxillary, and all isospondylous fishes have the maxillary participating in the gape. The fact that the Aplochitonidae (an isospondylous family) have the maxillary excluded from the gape, for all practical purposes, by the premaxillary does not necessarily mean close relationship with the Iniomid fishes, but it does indicate that the separation of the two orders on the basis of this single character presents difficulties.

As the general similarity between the myctophid-like inioms and the gonostomatid isospondyls (Suborder Stomiatoidea) has led many to regard the two groups as more closely related than ordinal separation would indicate, Marshall's (*15*: *54*) recent comparison of the swim bladders of the two groups is instructive (Table I).

Table I. Stomiatid and Myctophid Swim Bladders

	Myctophidae	Stomiatidae
Swimbladder type	Euphysoclist (with oval)	Paraphysoclist
Number of retia	Three	One
Type of rete	Unipolar	Bipolar
Position of rete	Anterior	Posterior

In view of the generally unsatisfactory nature of the iniomous-isospondylous separation discussed in the previous paragraphs, two hitherto unused means of distinguishing many of the Iniomi from the Isospondyli seem worth some mention here.

Among pre-isospondyls (holosteans) and the most primitive teleosts (*e.g. Elops*) there are two cross-commissures connecting the sensory canals running along the sides of the skull roof. One of these, the ethmoidal commissure (Nybelin, *18*), extends across the snout; the other, the supratemporal commissure, traverses the back of the skull roof. In modern iniomous fishes there is no ethmoidal commissure, but instead there is often a cross-connection between the supraorbital canals just behind the orbits. No evidence of such a cross-connection has been found in isospondylous fishes (*25*). In *Aulopus* this transverse canal is enclosed in the frontals for all but the median third of its length (Fig. 2 A). The amount of bone coverage in this genus seems to be independent of size, judging from an examination of specimens 3 to 15 inches long. In a

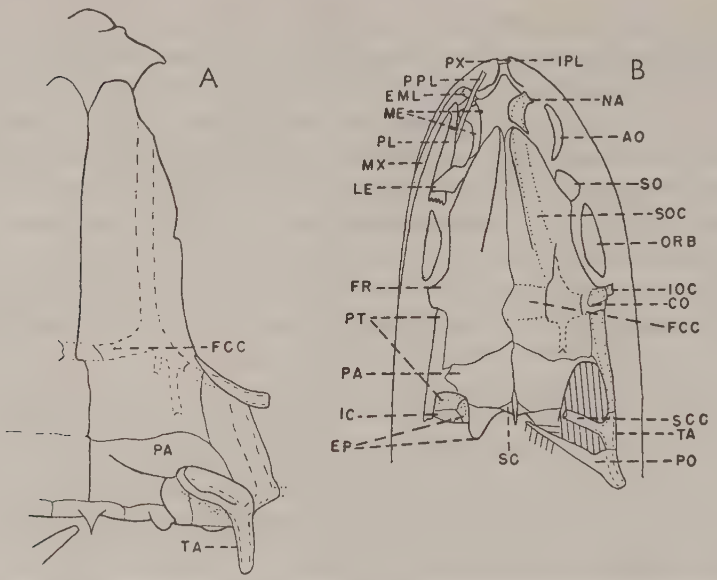

FIGURE 2. Top of skull of A, *Aulopus* and B, *Solivomer*. In B the sensory canals and certain superficial bones and muscles are shown on the right, the deeper bones and certain ligaments on the left. Sensory canals outlined with dashes have a bony roof; those outlined with dots lack a bony roof. Hatching represents musculature; stippled area, the floor of the post-temporal fossa. AO, antorbital; CO, posteriormost circumorbital; EML, ethmoid-maxillary ligament; EP, epiotic; FCC, frontal sensory canal commissure; FR, frontal; IC, intercalar; IOC, infraorbital sensory canal; IPL, interpremaxillary ligament; LE, lateral ethmoid; ME, mesethmoid; MX, maxillary; NA, nasal; ORB, orbit; PA, parietal; PL, palatine; PO, post-temporal; PPL, palatine-premaxillary ligament; PT, pterotic; PX, premaxillary; SC, supraoccipital; SCC, supratemporal sensory canal; SO, supraorbital; SOC, supraorbital sensory canal; and TA, tabular.

skull of *Synodus* this commissure is completely embedded in, and enclosed by, the frontals; in *Saurida* it is covered to about the same extent as in *Aulopus*; but in *Harpadon* it seems to be represented by a large, flesh-covered median depression. In *Parasudis* and *Bathysauropsis* only about a fifth of this cross-channel is covered by bone, and in *Chlorophthalmus* even less. In *Neoscopelus* and *Solivomer* (Fig. 2 B) only the lateral portions of this commissure have a bony roof, and in *Lampanyctus* there is merely a narrow, arched bony bridge over the point of exit of this commissure from the supraorbital canal on each side. In *Sudis* there is the same sort of opening from the inside of each supraorbital canal as in *Lampanyctus*, but it is obvious that the cross-commissure is incomplete because the skull between these two openings is tightly covered by a thin skin.

The final difference lies in the pelvic osteology. Under the base of the several innermost rays in most of the isospondylous fishes examined, there is a bony or cartilaginous nodule (pterygiophore) with which these pelvic rays movably articulate (Fig. 3 A, B); in a few this nodule is lacking, and the unmodified rays seem to articulate directly with the pelvic girdle. By contrast, in the great majority of iniomous fishes examined (*Aulopus*, *Saurida*, *Chlorophthalmus*, *Solivomer*, *Lampanyctus*, and *Lestidium*), this pterygiophore has become fused with the base of the bottom half of the innermost pelvic ray (Fig. 3 E, F). It thus appears in these fishes as if the two or three rays lateral to the innermost ray movably articulate with the base of that ray. That this differentiation between the iniomous and the isospondylous fishes does not always hold is demonstrated in *Alepisaurus* (Fig. 3 D) and *Bathypterois* (Fig. 3 C); in the former, the lower half of the innermost ray seems to be rigidly attached to, but not fused with, the pterygiophore, and in *Bathypterois*, the two elements form a movable articulation as in the isospondylous fishes.

With this background, some general discussion of the validity of ordinal recognition for the Iniomi seems in order. The present authors, like those who have studied the internal structures of iniomous fishes before them (*14*; *19*; *20*; *23*), are convinced of the integrity of the group. Though there is apparently no one feature that will separate all iniomous from all isospondylous fishes, this is hardly surprising in two such large and varied groups, groups which are not only an expression of very early teleost ("explosive") evolution but which have many similarities in habitat. Of greater significance to the question of the monophyletic *vs.* polyphyletic nature of the iniomous fishes would seem to be the whole series of functionally unassociated characters among those noted above that will separate large groups of inioms from all, or all but a few, peripheral forms of Isospondyli. By contrast, those ichthyologists who have apparently viewed the iniomous fishes as a series of independent offshoots from the Isospondyli (*6*) have concentrated their attention on one or a few external similarities, *e.g.* the photophores of the isospondylous gonostomatids and the iniomous myctophids, which can probably better be explained as parallel or convergent adaptations to a similar environment.

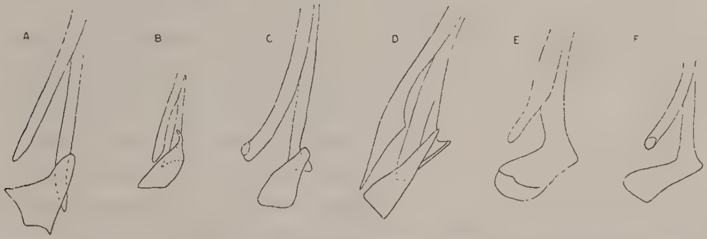

FIGURE 3. Innermost right pelvic ray and pterygiophore, viewed from above, with the head of the fish toward the bottom of the page. The more lateral pelvic rays that movably articulate with the same pterygiophore are not shown. A, *Pterothrissus*; B, *Yarrella*; C, *Bathypterois*; D, *Alepisaurus*; E, *Aulopus*; and F, *Solivomer*.

As to the relationships of the Iniomi, there is no known reason to doubt an ultimate isospondylous or proto-isospondylous origin for this group. However, the presence of post-temporal fossae in the skull and of fulcral scales in front of the caudal fin of the basal iniom *Aulopus* makes it impossible to derive this genus or the Order to which it belongs from any modern isospondylous fish higher than the elopoids. This merely points in the same direction as knowledge obtained from the fossil record—that the inioms have constituted an independent group, at least since the Cretaceous.

Relationships among the Families of Iniomi. The Order Iniomi is frequently divided into the Suborders Myctophoidea and Alepisauroidea. The Myctophoidea includes bathypelagic groups, such as the Myctophidae and Scopelosauridae, as well as benthonic families; the Alepisauroidea are wholly pelagic and bathypelagic. The anatomical differences between the representatives of these Suborders may reflect differences in environment as much as in ancestry, and since clear-cut characters that will unequivocally separate the two groups have yet to come to light, no formal recognition of these Suborders will be attempted here. But as groups of families, the "myctophoid inioms" and the "alepisauroid inioms" are meaningful.

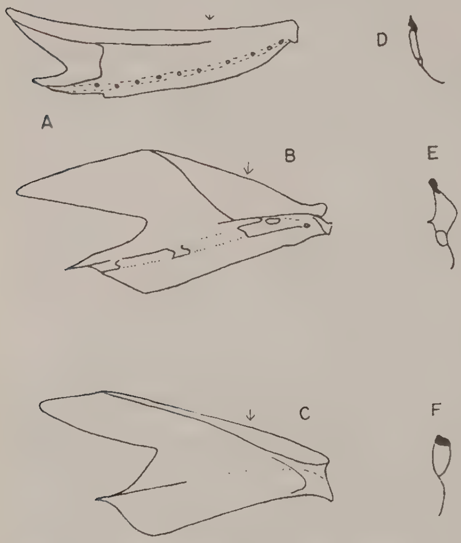

FIGURE 4. Right dentaries of A, D, *Synodus*, B, E *Chlorophthalmus*, and C, F *Neoscopelus*, from outside (A, B, C) and in cross section from front (D, E, F) at the points marked with the arrows in A, B, C. Parts of sensory canal roofed by bone indicated with dashed lines; unroofed portions dotted.

In the following *Synopsis* of *Families* (p. 15), the family Aulopidae is separated from the rest of the inioms because of its position near the basal stock from which the rest of the Order arose. The aulopids, together with the families included under 2 a, are the myctophoid inioms.

THE MYCTOPHOID INIOMS. Some comments regarding the characters used in the myctophoid section of the *Synopsis* seem needed.

The genera examined that have the mandibular canal completely enclosed in the dentary except for the pores are *Aulopus*, *Synodus* (Fig. 4 A), *Saurida*, *Harpadon*, *Bathysaurus*, *Ipnops*, *Bathypterois*, and *Bathytyphlops*. In the members under 6 b (Chlorophthalmidae, Neoscopelidae and Myctophidae), the mandibular canal either runs through long nonenclosed sections, as in *Bathysauropsis*, *Chlorophthalmus* (Fig. 4 B), *Parasudis*, and *Scopelosaurus*, or in a trough that is covered externally only by skin, except anteriorly, as in the myctophid-like fishes (Fig. 4 C) and the alepisauroids.

A related feature of dentary structure has to do with the shape of its outer surface in cross section. In the first group the lower rims of the dentaries of the two sides point toward each other, as in Fig. 4 D. In the second (Fig. 4 E, F), the lowermost portions of the dentaries on the two sides tend to project vertically downward parallel with each other (this characteristic only slightly developed in *Parasudis*).

As to the branchiostegal rays, in the available members of the first group they number 11 or more (except in *Bathysaurus mollis* with 8) and tend to be somewhat crowded at the front of the ceratohyal. In available members of the second group, they number 10 or fewer and are never crowded on the front of the ceratohyal, even though they sometimes extend forward onto the hypohyal of *Solivomer* and *Lampanyctus* (*14*: 333).

Whether the branchiostegal ray number and the features of the dentary bone are functionally correlated is not clear. In the case of the rays, arguments could be advanced for or against such a relationship, but to do so would seem almost pure speculation, since very little is known regarding the functional significance to the fish of small differences in its branchiostegal ray number. The functional significance of the dentary bone features seems far less equivocal. The bony enclosure of the sensory canal and the extension toward each other of the lower portion of the dentaries on the two sides would both serve as protection from abrasion on the bottom. Most of the fishes in which these features occur are bottom forms, and the synodontids, at least, habitually bury themselves in the sand.

On the other hand, a dentary with a sharp, thin, vertical lower rim and an enlarged, trough-like mandibular canal would not only present a delicate sort of chin structure to a bottom-living fish, but in the lightening of bone it would help to lessen the weight of a midwater form.

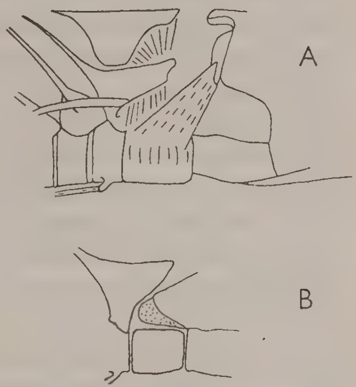

FIGURE 5. Region of first vertebra of *Solivomer*. In A the various membranes are shown by dashes; in B the membranes have been stripped away from the rubbery cylinder that separates the skull from the first ossified centrum; the cartilaginous cap to the exoccipital has been stippled.

Thus the primary differentiation used here would seem to be an adaptive one, separating a benthonic group from partially or primarily midwater forms. In making this generalization it is not assumed that all forms in the first group continually rest with their chins against the bottom or that no members of the second group are benthonic, but merely that an ancestral way of life has stamped its imprint on certain morphological structures in both groups, whatever the habitat of the particular form may be today. The chief difficulty with the above assumption concerns the chlorophthalmids; these are undoubtedly bottom forms, and it is difficult to see why they should lack the dentary and branchiostegal characters of the other benthonic groups.

Tacit in the arrangement provided here is the assumption that the iniomous fishes were originally a benthonic group. Perhaps this assumption is influenced unduly by the fact that the present benthonic *Aulopus* is more primitive, at least in certain respects, than other living iniomous fishes. Nevertheless, there are certain features in many or most of the iniomous fishes that at least suggest adaptations to a benthonic existence. One of these is the sensory canal commissure in the frontals; this might be a method of increasing perceptiveness to phenomena occurring overhead. Again, the consolidation of the pelvic skeleton might be associated with abrasion of the pelvic fins on the bottom.

According to the present arrangement, the first division contains three groups:

Aulopus, the synodontid-like fishes, and the bathypteroid-like fishes. *Aulopus*, as already noted, has certain features in which it is more primitive than the other two groups, indeed, more so than all other iniomous fishes.

In the bathypteroid-like category is placed a series of uncommon deep-water species. All appear to have broad flat heads with the eyes either small or highly modified. The gape is as large as, or larger than, that of synodontids, but the jaws and dentition are of a quite different type, lacking the synodontid specializations.

A second division is characterized by the single row of teeth on the premaxillary. This is admittedly a character of little systematic significance; at least two families in which the teeth are usually in bands have genera with a single row of premaxillary teeth: *Trachinocephalus* in the Synodontidae and *Parasudis* in the Chlorophthalmidae.

The basal members of the myctophid stock—*Solivomer*, *Neoscopelus*, and *Scopelengys*—are certainly related to the chlorophthalmids, as Regan noted (*23*). Indeed, it is rather difficult to find osteological characters to separate the two groups. In addition to the features mentioned in the *Synopsis*, both have the following two characteristics in common.

In all of the myctophid-like fishes dissected (*Solivomer*, *Neoscopelus*, *Electrona*, and *Lampanyctus*) and in the chlorophthalmids, the roof on the post-temporal fossa is reduced to a slight ledge and the body musculature extends forward over it onto the roof of the cranium (Fig. 2 B). As a result of this, such supratemporal commissure ossicles as may be present (TA of Fig. 2 B) are separated from the cranium by a layer of musculature. This is quite different from the situation in *Aulopus* (Fig. 2 A) and in the synodontids in which the body musculature does not extend over the roof of the post-temporal fossa and does not separate the supratemporal bone from the cranium. It is noted that *Aulopus* is the only iniomous fish in which both the roof and the lateral walls of the post-temporal fossa are intact; in the synodontids the lateral walls are lacking though the roof is present.

In *Aulopus* and *Synodus* the first vertebra articulates with the skull in the usual manner. However, in *Solivomer* (Fig. 5), *Neoscopelus*, *Scopelengys*, and the chlorophthalmids (but not apparently in such myctophids as *Electrona* and *Lampanyctus*), there is a curious gap in ossification between the skull and the first ossified vertebral centrum, somewhat reminiscent of certain isospondylous stomiatoids. This gap attains its greatest extent in *Solivomer*, where it is nearly equal to the width of the two centra following it; however, it remains very largely roofed over by the exoccipitals, which project backward from the skull, and by the first neural arch, which lies mostly forward of its centrum. In *Solivomer* this gap is filled by a rubbery membrane (the coat of the notochord?) which is attached by a strong membranous sheath to both the exoccipitals and the first neural arch (Fig. 5). Presumably the whole structure is a development of the intervertebral (notochordal) disc between the skull and the first centrum.

A similar if less well-developed gap in ossification occurs at least in *Bathypterois*; and some of the bathypteroid-like fishes have the body muscles extending well forward over the back of the skull roof, *e.g. Bathytyphlops*. These features strengthen Parr's (*20*) postulate of a relationship between the bathypteroids and the chlorophthalmids. The present authors would merely disagree with Parr in suggesting a derivation of the chlorophthalmids (and myctophid-like fishes) from some bathypteroid ancestor rather than vice versa.

Two comments are added concerning the general structure of the *Synopsis* and the arrangement of groups proposed below. First, a "basal" group could have been separated from a peripheral series at several levels. For example, a primary division could have been established, separating *Aulopus* from all other iniomous fishes; at the other extreme, the usual division of Myctophoidea and Alepisauroidea may well be a separation of the same type.

Finally it is noted that the present arrangement differs from that of Regan (*23*) chiefly in separating *Scopelosaurus* from the aulopids and in the classification of Regan's "Sudidae". The *Scopelosaurus-Aulopus* matter must remain without comment for reasons that have already been discussed; Regan's "Sudidae" has long been known to be heterogeneous. As for Parr's (*20*) classification, if one were to leave out of Parr's fig. 1 the families that are not considered here, there would be little difference between it and the present arrangement.

THE "ALEPISAUROID" INIOMS. Unlike the Myctophoidea, which includes both benthic and bathypelagic fishes, the alepisauroids are confined to the midwaters of the deep oceans. They are predatory fishes, ranging in length from a few inches to at least five feet, with certain structural features and trends, the whole forming a character complex that sets them apart from their myctophoid relatives.

The Alepisauroidea have been defined (*14*: 304) as ". . . bathypelagic Iniomi with no swimbladder or luminescent organs,[6] with a single row of numerous (more than 20) small teeth on each premaxillary, one or two rows of teeth on each palatine, one to three rows of teeth on each dentary and with gillrakers in the form of spines or teeth. The anal fin has from 12–50 rays and is usually set close to the caudal. Lastly, there are 3–4 + 4–5 branchiostegal rays." There is also a tendency in the alepisauroids for the pectoral fins to be ventral rather than lateral in position and for the basal axes of these fins to make an angle of less than 45° with the longitudinal axis of the body. Furthermore, with few exceptions, the skeleton is reduced in varying degrees. Certain of these characters will now be considered.

At no time during the life history of any alepisauroid does there appear to be any vestige of a swim bladder. Among the myctophoidranioms, this organ is commonly present in the Myctophidae and in *Neoscopelus* (*13*; *15*).

The skeletons of most alepisauroids are lightly ossified, a good indication of the lack of calcification being the long time of exposure needed to obtain tolerably clear hard-tube radiographs. The delicacy of much of the skeleton is also readily appreciated during the handling of these fishes. Further, there is considerable evidence in some alepisauroids that the calcification of the skeleton is a slow and protracted process (*14*: 304).

The lack of a hydrostatic organ and the reduction of bony substance in the skeleton have been regarded as correlated features rather than as a reduction of bony substance caused by diminished availability of vitamin D in the deep-sea environment (*14*: 304). Quantitative expression of this contention is to be found in recent work by Denton and Marshall (5) on the buoyancy of bathypelagic fishes without a gas-filled swim bladder. These authors found that *Gonostoma elongatum* and *Xenodermichthys copei* were only slightly heavier than sea water, their near-neutral buoyancy being largely due to the reduction of the two densest tissue systems of the body—muscle and skeleton. If this is true of these two species, it is likely that very similar results would be obtained for most alepisauroids.[7]

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[6] But see footnote 9. For fuller treatment of the Alepisauroidea, see Marshall, *14*: 304.

There is thus some reason to believe that, despite their lack of a swim bladder, alepisauroid fishes are able to maintain their level in the ocean with relatively little effort. But, as Denton and Marshall have pointed out, a fish cannot have a reduced framework and musculature and still be a tireless hunter. It is thus hardly surprising that the form and fin pattern of alepisauroids suggest that they have a hovering and darting, pike-like way of securing their food. During recent bathyscaphe dives, one species, possibly *Paralepis rissoi*, was observed to hover vertically in the water, usually head uppermost (7). Furthermore, some of the alepisauroids (*Evermannella*, *Omosudis*, *Anotopterus* and *Alepisaurus*) are able to take a large meal at one fell swoop (*14*: 304).

Apart from the low level of ossification of the skeleton, many alepisauroids have a very reduced squamation. The skin of *Omosudis*, *Alepisaurus*, and *Evermannella* is completely scaleless, while *Anotopterus* has scale-like segments only above the lateral line. The Scopelarchidae bear scales on the cheeks, gill covers and body. In the Paralepididae there appears to be considerable diversity in the degree of squamation (*10*). The species of *Paralepis* and *Notolepis* have fully scaled bodies, but in *Lestidium* and *Macroparalepis* all or most of the scales are missing. In *Sudis* the scalation is confined to the skin covering the preopercula.

Reduction or loss of scales will certainly mean some lowering of density. But Marshall (*14*: 304) has suggested that the distensibility of tissues required to accommodate large prey in the body cavity precludes the development of an overlapping type of squamation. Fishes other than the alepisauroids that are known to swallow large prey (melanostomiatids, *Chauliodus*, *Idiacanthus*, *Malacosteus*, Lyomeri, Giganturoidea, *Chiasmodon* and *Melanocetus*) are certainly either without scales or have a nonoverlapping type of squamation. This statement is also true of one fish, *Parataeniophorus gulosus*, that was much distended by an enormous meal of small prey (copepods) (*1*).

As already mentioned, *Alepisaurus*, *Omosudis*, *Anotopterus* and *Evermannella* are able to engulf relatively large prey, and these are the alepisauroids without body scales. There is no record of any scopelarchid being distended by a large meal, although they certainly have a formidable dentition. Little is known of the food of the Paralepididae, but one species without body scales (*Notolepis coatsi*) may become bloated from a surfeit of krill (*Euphausia superba*).

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[7] A five-foot *Alepisaurus ferox* weighs about four pounds (*12*), a weight that is attained at a length of about two feet by the pike (*Esox lucius*).

Intermuscular bones are developed in both epaxial and hypaxial parts of the myotomes of *Alepisaurus*, *Anotopterus*, *Omosudis* and of certain Paralepididae (Fig. 6). Marshall (*14*: 304) was unable to find intermuscular bones in the Scopelarchidae and Evermannellidae, although Parr (*20*) stated that epineural bones are present in the first family. Under the Evermannellidae he made no mention of these bones, but it may be that further examination would reveal their presence.

There are both parallel and divergent features in the fin patterns of alepisauroid fishes. Considering first the divergences, the dorsal fin is the most diversely developed. It is entirely absent in *Anotopterus*, but in *Alepisaurus* it is both extensive and high, originating just behind the head and spanning about two-thirds of the standard length. In other alepisauroids the dorsal fin is set about halfway down the body length or is nearer to the caudal fin than to the head, and is relatively short-based.

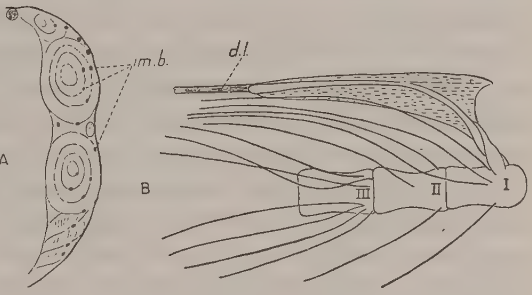

FIGURE 6. A, transverse section through the trunk muscles of *Anotopterus pharao*, showing the intermuscular bones (im. b.); B, some of the larger intermuscular bones associated with the first three vertebrae of *Omosudis lowei*; d. l. = dorsal ligament. Both from N. B. Marshall, *14*: 330.

The pectoral, pelvic and anal fins follow a more uniform structural plan.[8] In nearly all alepisauroids the pectoral fin is inserted below the longitudinal axis, and the angle between this line and that through the pectoral base is generally less than 45°. Marshall (*14*: 304) suggested that there might be some connection between such an insertion of the pectoral and the position of the anal fin, which is usually close to the caudal fin. During swimming, the lateral movements of the postanal part of the body might be expected to generate a lift force, the anal fin acting like the larger lobe of a shark's caudal fin. The concomitant depression of the fore part of the body could be countered by a paravane-like setting of the pectoral fins, one function of which could be to raise the head, the resultant thus being a lift about the fish's center of gravity. As it seems likely that alepisauroid fishes are slightly heavier than sea water (p. 10), such means of overcoming a steady sinking during swimming would be advantageous in these bathypelagic fishes.

The pelvic fins of the Alepisauroidea are abdominal in position, and there is a definite tendency for each fin to have nine rays. Variation in the number of pelvic rays seems to be greatest in the Paralepididae, the range being 8 to 12 (*10*).

Except for *Evermannella normalops* Parr, the eyes of the Scopelarchidae and Evermannellidae are tubular in form, and the optical axes of the adults are directed upward. All other alepisauroids have the usual type of fish eyes. With regard to the development of tubular eyes in diverse groups of deep-sea fishes, the common possession of such visual organs might be no certain indication of relationships. In the deep-sea environment, tubular eyes must endow their possessors with certain visual advantages, and there would seem to be only this one structural way of producing a great increase in binocularity in vertebrates with laterally placed eyes. However, these two families have certain other common features that have been considered by Parr (*20*). Perhaps the outstanding osteological similarity is that the parietals appear to have fused with the frontals, whereas in other alepisauroids the parietals are separate ossifications. The body is short to moderately elongate and the anus is either near the origin of the anal fin or midway between the pelvic and anal fins. The Alepisauridae, Omosudidae, Anotopteridae and the Paralepididae have rather elongate to very elongate body shapes, and the anus is nearer to the insertion of the pelvic fins than to the origin of the anal fin.

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[8] Regarding the position adopted during hovering, nothing in the fin pattern of *Paralepis rissoi* might suggest that it would "stand on its tail" (see p. 10).

Concerning these four families, Harry (*10*) considered the Paralepididae to be most closely related to the Anotopteridae, both having "... the same general proportions, essentially similar osteology, the same peculiar cartilaginous development of the jaws, which is found in these two families alone in the order, and a good number of other similarities." One of the most striking of the last category is the development of scale-like ossifications along the lateral line.

The Alepisauridae and Omosudidae are certainly more closely related than is either family to the Anotopteridae or the Paralepididae. Regan (*23*) observed that *Omosudis* has the head, mouth and teeth very much like *Alepisaurus* and that both genera have completely lost the scaling, even along the lateral line. Parr (*20*) saw no reason to doubt Regan's opinion.

The alepisauroid織 inioms are not readily defined, lacking clear-cut diagnostic features such as delight the systematist. Certain of their common characters might seem to be subsumed by convergent evolution. Without a hydrostatic organ, neutral buoyancy can be approached only by reduction in the skeletal and muscular systems, which may have led to convergence of fin patterns (see p. 11). In turn, such reduction in propulsive powers may have entailed convergence towards pike-like forms and habits (see p. 10). Again, the development of gill rakers as teeth or spines could be no more than parallel adaptations to a predatory life. Gill rakers of this type are found in the Synodontidae, Bathysauridae, and Harpadontidae, which are the most rapacious of the myctophoid fishes.

Such problems are not easily resolved, but comparison with the Scopelosauridae provides some insight. In body form and in certain features of the fin pattern, the scopelosaurids have a striking resemblance to the paralepidids. Yet the scopelosaurids are myctophoid rather than alepisauroid fishes, having lateral pectoral fins (with fin angles of more than 45°) and lath-like gill rakers. (See also under Scopelosauridae, p. 194).

These considerations and others (*14*: 304) show that the "Alepisauroidea" is at least a useful taxonomic grouping. After considerable acquaintance with the group, one even gets the impression (partly intuitive and aesthetic) that it may be a natural one. If this is granted, what are the relationships of the alepisauroid inioms to the other iniomous fishes? The first known representative of a recent alepisauroid (the paralepidid *Holosteus*) is from the Eocene, but the fossil record does not appear to be very helpful (*10*).

The most generalized alepisauroids seem to be the scaled genera of the Paralepididae. The Anotopteridae, Alepisauridae and Omosudidae are clearly more specialized than *Paralepis* or *Notolepis* (in loss of scales, highly modified dentition, etc.). The Scopelarchidae have certain generalized features, such as well-developed scaling, circumorbital bones, and upper jaw bones, but in ocular, dental and osteological characters they display considerable specialization in comparison with *Paralepis*. An outstanding primitive paralepidid character is the presence of large parietal bones which meet in front of the supraoccipital (*20*).

If the most generalized alepisauroids are the scaled paralepidids, as seems reasonable, how do these fishes compare and contrast with their counterparts among the myctophoid inioms? It would appear that *Paralepis* and *Notolepis* have no outstanding relationship to either the Aulopidae or the Chlorophthalmidae but come closest to the latter. In branchiostegal-ray complement (usual number 8, equally divided between the epihyal and ceratohyal) there is a close fit. Harry (*10*) has even claimed that "The paralepidids from the Miocene diatom beds at Lompoc, California, and *Parascopelus* from the Miocene of Europe appear to provide a complete intergradation between this family and the Chlorophthalmidae." However this may be, it is certain that fuller appreciation will not be possible until more is known of the anatomy of both families. Such knowledge is particularly lacking about the Chlorophthalmidae.

Luminescense. The lantern fishes (Myctophidae), *Neoscopelus*, and two paralepidids possess definite light organs. In the Myctophidae (p. 190), photophores are usually well developed and are frequently species- or sex-specific. In the two paralepidids, the luminous tissue is localized in two bands above the abdomen.[9] Luminosity has been reported in four other species, but in none has this feature been substantiated. The celebrated dorsal "eye" of *Ipnops* (p. 150) was thought to be a luminous organ for over 50 years, but the recent study of a specimen caught by the GALATHEA has shown it to be a highly specialized photoreceptor (*17*). Luminosity in *Scopelosaurus* (p. 197) has not been reconfirmed, and Harry[10] has refuted Gilbert's account (*8*) of a photophore along the lower margin of the orbit of *Lestidium nudum*. It has been reported that *Harpadon*, when newly taken, is brilliantly luminescent, but those more familiar with these fishes believe that the luminosity occasionally encountered here is of bacterial origin (*21*).

Breeding and Development. Information on the reproduction and development of the Iniomi is scant. The young stages of certain forms are known: the pelagic and bathypelagic species of the alepisauroid inioms and the myctophoid families (Myctophidae and Scopelosauridae); and some of the more inshore representatives of the benthonic forms such as the lizardfishes and allied species (Synodontidae, Aulopidae and Harpadontidae). References to descriptive accounts of the young of the various species will be found in the discussions of the species that follow. These fishes probably follow the reproductive pattern thought to be most common in the sea: eggs developing in the surface waters, the larvae continuing a pelagic life until metamorphosis, then descending to a bottom or bathypelagic existence.

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[9] *Lestidium prolixum* Harry and *Lestidium japonicum* Tanaka; see Haneda (*9*).

[10] The classification of the iniomous fishes. Circular, Amer. Soc. Ichthyol. Herepetol., 48 pp. mimeo., n.p., n.d. This most useful compilation has never been officially published.

In several groups, however, neither fertilized eggs nor larvae are known. To these groups belong the deep-water, bottom-restricted species (Bathypteroidae, Bathysauridae, Ipnopidae, *et al.*), and it seems possible that the eggs and larvae develop either on the bottom, or bathypelagically near the bottom. The evidence is negative but none the less persuasive. First of all, we have but recently learned of the presence of adult bathypteroids in the central Mediterranean,[11] which is one of the most intensively studied bodies of water in the world. In few areas have studies of the development of fish eggs and larvae been so thorough,[12] yet even here the eggs and young of the bathypteroids remain unknown. The number of eggs spawned by a single adult is also suggestive. Egg counts on the rarer benthonic inioms have not been generally made, but an average bathypteroid, a 139-mm *Bathypterois* (*Bathypterois*) *quadrifilis*,[13] living at a depth of 600 fathoms, contained about 4500 eggs. Epipelagic development would imply that these eggs would rise or be carried upward through a water column about three-fourths of a mile high, hatch and develop in the surface, descend through this water column for the same distance and by chance reach a bottom area amenable to adult life. This number can be compared with the 2,000,000 eggs that a 40-inch haddock produces annually (*3*) or with the 25,000 to 40,000 well-developed young cast annually by the viviparous redfish, *Sebastes marinus*. Even if *Bathypterois* spawns more than once a year, the difference in egg number and the severity of the environment suggest nonsurface development.

Several inioms show strong sexual dimorphism. In the Aulopidae, the males and females differ in fin form and length. In several species of lanternfishes (Myctophidae), the sexes can be distinguished by the photophore pattern, while in some other myctophids and some lizardfishes (Synodontidae) slight morphometric differences associated with sex can be found. But external sexual differentiation in form cannot exist in the absence of a strong or complete internal difference between the sexes, and recently many of the offshore inioms have been found to be hermaphroditic.

In a preliminary report (*16*), Mead noted the presence of an ovotestis in the families Chlorophthalmidae, Bathypteroidae, Alepisauridae, and Paralepididae. Certain of the Ipnopidae and *Bathysaurus* are also now known to be hermaphrodites. Because of the relative scarcity of these fishes and the present inability to obtain living individuals, no study of the reproductive behavior has been possible. It is of interest that hermaphroditism is common to the deep-water and offshore inioms which may be sparsely distributed. Self-fertilization may take place when another individual of the same species is not available for cross-fertilization. Certainly some of the benthonic inioms, rare and probably sluggish swimmers such as *Ipnops*, appear from trawl-haul data to be so sparsely distributed that the chance of accidental contact between individuals is slight. But not all hermaphroditic inioms are sparsely distributed, for such benthonic forms as *Parasudis truculentus* and the species of *Chlorophthalmus* are extremely abundant in certain places, and at least one of the pelagic alepisauroid inioms (*Alepisaurus ferox*) is thought to school (p. 486).

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[11] See references under *Benthosaurus* "*amblyops*" and *Benthosaurus* sp. on p. 122.

[12] See, for example the "Uova, larvae, e stadi giovanili di Teleostei" which comprises monogr. 38 of the "Faunae Flora d. Golfo de Napoli," and the extensive series of papers in the "Mem. R. Comitato Talassografico," Messina.

[13] OREGON St. 1426, 29°07′N, 87°54′W, Sept. 24, 1957.

Distribution. With the exception of the estuarine species of *Harpadon*, all iniomous fishes are marine and nearly all occur in deep water. The bottom-living marine representatives include the lizardfishes, some of which live as far inshore as the intertidal zone, and the ipnopids, some of which have been caught between 5000 and 6000 m, depths beyond which but few fishes of any description are known. Other benthic inioms can be found at all depths between these extremes. The pelagic families of myctophoid inioms are also found in deep water, for the Myctophidae, some of which are known to migrate vertically, live from the surface to a depth of about 2500 m.

The alepisauroid inioms are pelagic, and none normally lives over the continental shelf. Their depth range is from the surface to about 2500 m.

Synopsis of Families. The following *Synopsis of Families* represents a classification of those here included within the Iniomi and presented in a "natural" sequence. Since the characters used here, though of apparent evolutionary significance, are technical and in many instances internal, the reader is referred to the *General Key to Families* in Part 3 (pp. 97–104) for a more helpful aid to the identification of specimens.

Synopsis of Families

1a. A well-developed, horizontally aligned bony plate, *i.e.* fulcral scale, in the flesh of the caudal peduncle just ahead of the anteriormost procurrent caudal rays above and below; post-temporal fossa in rear of skull present; two supramaxillaries. Aulopidae, p. 19.

1b. No bony fulcral scales in front of the caudal fin; no post-temporal fossa; one supramaxillary or none.

  2a. Teeth in premaxillary in multiple series or in a band of variable width (except *Parasudis* and *Trachinocephalus*).

    3a. Teeth and gill rakers needle-like and usually lance-shaped; maxillary reduced or absent, not expanded and flattened posteriorly; circumorbitals behind the eye expanded to form a strut for the support of the upper jaw.

      4a. Head and body with scales.

        5a. Scales of lateral line not enlarged. Synodontidae, p. 30.

        5b. Scales of lateral line enlarged. Bathysauridae, p. 103.

      4b. Head and body naked save for a series of scales along lateral line and on tail. Harpadontidae. Indopacific.

3b. Teeth not needle-like or lance-shaped; gill rakers of the usual lath-like shape; maxillary not reduced but normal in appearance and with its posterior end broad and flattened in the usual way, or at least expanded and club-shaped in appearance; circumorbitals behind the eye not forming a strut for the support of the upper jaw; eyes minute and probably nonfunctional, or virtually absent.

6a. Mandibular sensory canal enclosed in the dentary except for the large pores to the exterior (Fig. 4 A); outer surface of the dentary (in cross section about halfway along its length) either convex or flat (Fig. 4 D).

7a. Pectoral fin divided into two distinct parts; eye minute and laterally-directed, located just above upper jaw; gill rakers of the usual lath-like shape. Bathypteroidae, p. 114.

7b. Pectoral fin not divided into two parts; eye minute, laterally directed, and situated immediately above upper jaw, or absent from this location, the photoreceptor represented by a pair of large, broad plates which are yellow in life and roofed by the frontal bones; gill rakers of the usual lath-like shape, or completely absent save for the single raker at the angle of the arch. Ipnopidae, p. 147.

6b. Less than half of the mandibular canal in the dentary enclosed in bone (Fig. 4 B, C); outer surface of the dentary (in cross section halfway along its length) more or less concave (Fig. 4 E, F; except *Parasudis*).

8a. Snout depressed; nonluminous; without swim bladder. Chlorophthalmidae, p. 162.

8b. Snout compressed; usually luminous; swim bladder usually present.

9a. Supramaxillary absent. Myctophidae, p. 190.

9b. Supramaxillary present. Neoscopelidae, p. 192.

2b. Teeth in premaxillary in a single series.

10a. Gill rakers of the usual lath-like shape. Scopelosauridae, p. 194.

10b. Gill rakers usually reduced to teeth or spines.

11a. Eyes normal in form, not tubular; parietals not fused to frontals; anus much closer to insertion of pelvic fins than to origin of anal fin.

12a. Dorsal fin present, its base less than half the length of the fish.

13a. Dentary without a single, enormously enlarged fang;

head and body with or without scales, but always with a series of shield-like ossifications along the lateral line. Paralepididae, p. 205.

13b. One enormously enlarged fang in each dentary; palatines with enlarged fangs; head and body without scales. Omosudidae, p. 462.

12b. Dorsal fin present or absent, and when present, its base longer than half the length of the fish.

14a. Dorsal fin high and sail-like, spanning about two-thirds of length of fish. Alepisauridae, p. 482.

14b. No dorsal fin. Anotopteridae, p. 498.

11b. Eyes tubular in form and directed upward (except in *Evermannella normalops* Parr); parietals fused to frontals; anus near origin of anal fin or midway between pelvic and anal fins.

15a. No teeth on tongue. Evermannellidae, p. 511.

15b. Teeth on tongue. Scopelarchidae, p. 566.

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COASTAL OCEANOGRAPHY IN THE GULF OF MAINE, 1962-65

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Distributions of temperature, salinity, water transparency and currents were determined from 21 stations located from the headlands to 28 kilometers offshore, and from Cape Ann, Massachusetts (42°41′ N, 70°35′ W) to Machias Bay, Maine (44°40′ N, 67°20′ W).

Seasonal variations of temperature-salinity realtions were examined by grouping the data into 5 geographic areas along the coast. Arithmetic means were calculated for temperature and salinity data from the 4 to 5 stations within each area and seasonal diagrams plotted for the depths sampled: 0, 10, 20, 30 meters and bottom. In all areas temperature increased with vernal warming and salinity was reduced by spring river dilution to its seasonal low (29.7‰). By summer, temperature reached a peak (15.9° C.) and salinity began to rise coincident with the decrease in runoff to the rivers. This rise in salinity continued into the fall and winter seasons when salinity was highest (32.8‰) and temperature lowest (0.2° C.). During all seasons there was an eastward reduction in the vertical ranges of temperature and salinity, and the water column to the east was more subject to mixing. This areal trend was especially marked in the spring and summer.

Isolines of temperature and salinity were contoured at the sampled depths for 11 cruises. The distributions of isolines were frequently interrupted from an alongshore pattern to one normal to the coast or into partial cells. Isolines of the Secchi disc reciprocal also were contoured for these cruises and supplemented with contours of extinction coefficients obtained during three cruises. Contours from both the Secchi disc reciprocals and the extinction coefficients departed from an alongshore pattern, but there was no apparent agreement between the distributions obtained by the two methods of measuring water clarity. Both had measurements recorded primarily between 0.100 and 0.300, with the lower values present in the spring and summer; and the higher values during the fall and winter. Departures of the sampled variables from an alongshore contour pattern were found largely in the western sector of the coast where most of the river discharge occurred. In this sector, river mouths were evenly spaced and thus horizontal gradients fluctuated parallel to the coast.

Surface drift bottles, sea bed drifters, and calculations relative to the 30-meter depth were used to study currents. Recoveries of drift bottles indicated major features of the Gulf of Maine circulation: 1) a southerly flow along the western side of the Gulf in the winter, and 2) the development of the cyclonic gyre in the spring. Recoveries of sea bed drifters showed a shoreward compensatory bottom current. Contours of dynamic height anomalies, used only to approximate direction of flow, appeared as portions of eddies in the western sector associated with the temperature and salinity gradients which were especially well developed in the spring and summer. These were reduced during the fall and winter seasons. Contours in the eastern sector indicated an alongshore westerly current during all seasons.

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SECCHI DISC OBSERVATIONS AND EXTINCTION COEFFICIENTS IN THE CENTRAL AND EASTERN NORTH PACIFIC OCEAN

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SECCHI DISC OBSERVATIONS AND EXTINCTION COEFFICIENTS IN THE CENTRAL AND EASTERN NORTH PACIFIC OCEAN

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ABSTRACT

Measurements of submarine daylight were made with a photometer and Secchi disc and of water color with a Forel-Ule color scale during three summer cruises in the central and eastern North Pacific Ocean. The relationships between extinction coefficients, reciprocals of Secchi disc readings, and color observations were determined and their applications and limitations are discussed. It is concluded that the disc is a useful tool, but that caution should be observed when extrapolating the relationship between Secchi disc measurements and extinction coefficients from one oceanic environment to another.

INTRODUCTION

The measurement of submarine daylight with a Secchi disc is subjective, yet Poole and Atkins (1929) show from data gathered in the English Channel that extinction coefficients for visible rays can be approximated by the ratio of 1.7 over the depth in meters at which the disc disappears from sight. This relationship is useful and can be found in publications dealing with the ecology of fishes (Murphy 1959) and organic productivity in the oceans (Ryther and Yentsch 1957; Riley 1956) and in lagoons (Zein-Eldin 1961). The purpose of the analyses given below is to make available similar relationships obtained from data collected in the central and eastern North Pacific Ocean and to demonstrate their applications and limitations.

The author is indebted to Mr. James W. McGary for his counsel concerning the collection and treatment of the data. Mr. Richard A. Barkley made helpful suggestions concerning analysis of the data, and Mr. Vaughn Anthony kindly reviewed the statistical approaches used. The author appreciates critical reviews of the manuscript made by Dr. Gordon A. Riley and Dr. Robert W. Holmes.

METHODS

The U.S. Bureau of Commercial Fisheries at Honolulu, Hawaii, routinely measured submarine daylight with a Secchi disc during exploratory fishing and oceanographic cruises in the central and eastern North Pacific. During certain of these cruises (*John R. Manning* 32, 36; *Hugh M. Smith* 52), measurements of submarine daylight were made with a photometer while a Secchi disc reading was obtained and water color was determined with a Forel-Ule color scale. The general areas covered by the cruises were between 175° and 145° W longitudes and the Hawaiian and Aleutian Islands, and along the North American west coast from the State of Washington to Baja California. Sampling occurred over the late spring to early fall seasons. Details of the cruise tracks, sampling procedures, and instruments used were published by Callaway (1957), Callaway and McGary (1959), and Graham and Craig (1961). Measurements with a Schueler photometer were made at the 50-, 10-, 5-, and 1-% levels of transmission. The response curve of the photometer matched the standard curve of the International Commission on Illumination with a spectral range of 430 to 700 mμ and a peak sensitivity at 550 mμ. Secchi disc observations and water color determinations were made according to instructions in the U.S. Navy Hydrographic Publication 607 (1955), with the exception that the Secchi disc (30 cm diam) was retrieved to one-half the depth of a given observation rather than to 1 m

TABLE 1. *Relations of extinction coefficients* (κ), *Secchi disc reciprocals* (1/SD), *and Forel-Ule color scale measurements* (FC)

Cruise	Multiple regression formulae	Multiple correlation coefficients		Standard deviation from regression	Forel-Ule color omitted	Standard deviation
		R	$N-3$	3 variates	R^2-r^2	2 variates
Smith 52	$\hat{\kappa} = -0.0108 + 0.8248\ 1/SD + 0.0210\ FC$	0.83*	23	0.0172	0.162	0.0208
Manning 32	$\hat{\kappa} = +0.0253 + 0.2765\ 1/SD + 0.0211\ FC$	0.89*	39	0.0170	0.069	0.0207
Manning 36	$\hat{\kappa} = -0.0131 + 1.5584\ 1/SD + 0.0113\ FC$	0.89*	36	0.0142	0.055	0.0156
Manning 36 $\geqslant$17.22C	$\hat{\kappa} = +0.0395 + 0.3634\ 1/SD + 0.0085\ FC$	0.73*	18	—	0.026	
Manning 36 $\leqslant$17.16C	$\hat{\kappa} = -0.0079 + 1.2858\ 1/SD + 0.0132\ FC$	0.91*	15	—	0.082	

* Significant at the 1% level for R.

from the surface, and the Forel-Ule color scale was compared against the disc background.

Extinction coefficients were calculated after the manner of Sverdrup, Johnson, and Fleming (1942).

$$\kappa_\lambda = 2.30[\log I_{\lambda,z} - \log I_{\lambda,(z+1)}],$$

where: κ_λ is the rate of decrease (meters^{-1}) of downward-traveling light or the extinction coefficient. $I_{\lambda,z}$ and $I_{\lambda,(z+1)}$ are the radiation intensities for wave length λ at depths z and $z+1$. For the 10% level of transmission the intensities are 100 and 10%, respectively. 2.30 is introduced because logarithms to the base 10 are used.

This level was chosen because shading by the vessel rigging made the 50% level difficult to obtain, while the 5% level was below that at which other investigators generally found the Secchi disc to disappear from view (Clarke 1941; Gall 1949; Poole and Atkins 1929). The reciprocal of each Secchi disc observation was also obtained. Multiple regression formulae were then calculated for each cruise following the method of Snedecor (1946) for the three variates, extinction coefficient, Secchi disc reciprocal, and Forel-Ule color. The results of these calculations for stations occupied near 1200 hours are listed in Table 1.

RESULTS

Multiple correlation coefficients (R), shown in Table 1 for each cruise, are significant at the 1% level, indicating that the Secchi disc reciprocals and Forel-Ule color scale indices can be used successfully to estimate the extinction coefficients. Information provided by the Secchi disc and Forel-Ule color is not independent. Rather, they measure concurrent phenomena (Jerlov 1951) so that R is not greatly larger than r calculated for the Secchi disc information alone. This is indicated by the small percentage losses in success of estimation (R^2-r^2), accompanied by slight increases in the standard deviations from regression, when the color measurement is omitted from the calculations. Nevertheless, it is interesting to note that the greatest loss is shown by data from *Smith* Cruise 52, a spring and early summer cruise. The other data are from summer cruises. If water color, in part, is related to the concentration of phytoplankton, one would expect the contribution of the Forel-Ule color scale to be greatest in areas having some spring blooms. Upwelling, concurrent with available summer radiation, also subsequently would produce a concentration of phytoplankton (Sargent and Walker 1947).

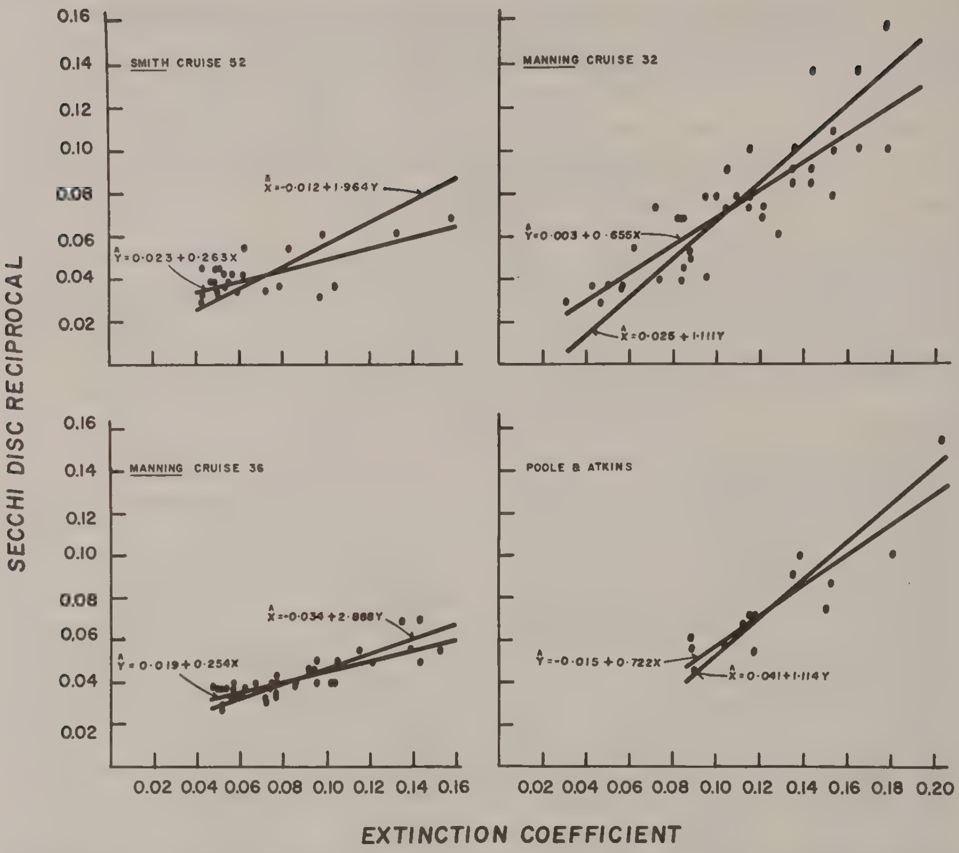

FIG. 1. Regression lines showing the relationship between Secchi disc reciprocals and extinction coefficients in the eastern and central North Pacific Ocean, and the English Channel (left, upper and lower right, respectively).

The upwelling is usually indicated at the surface by relatively colder water. During cruises *Manning* 36 and *Smith* 52 along the west coast, such areas of upwelling were present. Temperature data from the first cruise were sufficiently numerous and widespread (McGary, Graham, and Otsu 1961) to allow the segregation shown in Table 1. The loss of success ($R^2 - r^2$) was about three times that in the colder water.

Omitting Forel-Ule color determinations, the data and their corresponding regression formulae are plotted in Fig. 1 for cruises by the Bureau of Commercial Fisheries and measurements made by Poole and Atkins (1929) in the English Channel. Both equations are given and the spread between them is relatively small, indicating the close relationship between the two measurements. However, some of the regression lines do not contain the origin, and if this is true it could lead to inefficient estimates. This possibility was examined statistically after the method of Williams (1959). The assumption that the lines pass through the origin is not acceptable statistically at the 1% level for either equation in *Manning* Cruise 36 or in that estimating $\hat{Y}$ in *Man-*

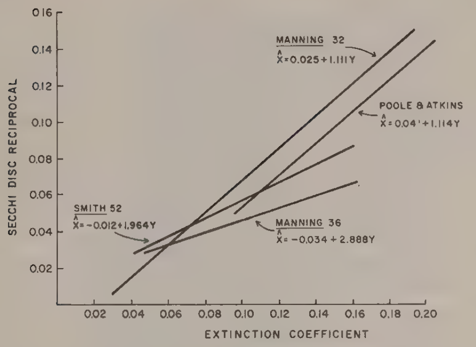

Fig. 2. Comparison of regression lines providing estimates of extinction coefficients from Secchi disc reciprocals shown in Fig. 1.

ning Cruise 52. Chauvenet's criterion (Worthing and Geffner 1943) was used to reject extreme values that might influence the data unduly. In one case, a single value and in two cases, two values were rejected. Recalculation of the data did not bring the intercepts significantly closer to the origin.

Another feature of Fig. 1 is the apparent differences in slope of the lines between the four groups of data. Differences between those lines estimating $\hat{X}$ are of special concern to this paper and they are presented together in Fig. 2. An analysis of covariance indicates that all of the lines cannot be fitted to a common slope ($F = 9.84$, $P\ 0.01 = 4.82$). The lack of agreement to a common slope is related mainly to the lower Secchi disc readings obtained in the eastern North Pacific Ocean for the upper range of extinction coefficients (Fig. 1). The slopes of data from the west coast (*Manning* Cruise 36, *Smith* Cruise 52) are not significantly different ($F = 0.03$, $P\ 0.05 = 4.00$) and those of the central North Pacific Ocean and the English Channel are obviously similar.

DISCUSSION

The processes involved in the extinction of submarine daylight are complex. The transparency of seawater is affected by molecular scattering, suspended particles, and dissolved colored substances. Molecular scattering is of importance in the clear blue and relatively barren oceanic waters while particles and dissolved substances are associated with more productive water. The distribution of particles and dissolved substances in a given area is largely determined by circulation features and influenced by thermocline structure (Kampa 1960; Boden, Kampa, and Snodgrass 1960). Each of the three North Pacific cruises by the Bureau of Commercial Fisheries sampled water varying from clear blue to turbid green. But the two areas investigated, the central North Pacific Ocean and along the west coast of North America, differ considerably in their circulation features. Along the west coast there are three major features: 1) A number of centers of upwelling occur during the spring and summer; 2) in the northeastern portion of the coast, river effluent influences light transmission; and, 3) the California Current flows southward along the coast. These circulation features are indicated in a plot of extinction coefficients (Fig. 3) obtained during a summer quasisynoptic northeastern Pacific Ocean albacore survey by two U.S. Bureau of Commercial Fishery vessels and seven chartered trollers (Graham 1959; Callaway and McGary 1959). Coefficients are calculated from photometer measurements made from the *Manning* Cruise 36 (Table 1), from Secchi disc and Forel-Ule color observations made from a second bureau vessel and calculated from the multiple regression formulae given for *Manning* Cruise 36 (Table 1), and from disc observations made on the chartered vessels and calculated from the regression formula given for *Manning* Cruise 36 in Fig. 2. Like the familiar current pattern in the northeast North Pacific Ocean, the isopleths split as they approach the west coast, one group following the southward flow of the California Current and the other northward into the Gulf of Alaska. The cells of high extinction coefficients (>0.16) near the coast are associated with areas of summer upwelling except for the most northern cell (>0.13) which

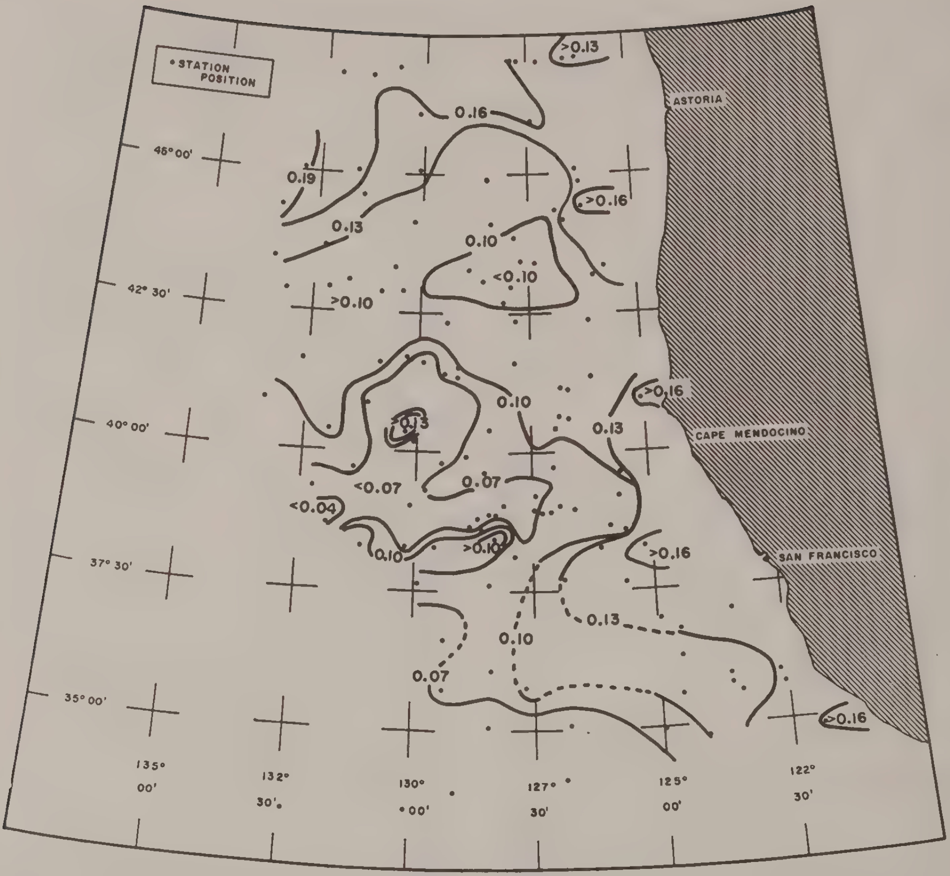
• STATION POSITION
ASTORIA
CAPE MENDOCINO
SAN FRANCISCO
45°00'
42° 30'
40° 00'
37° 30'
35° 00'
135° 00'
132° 30'
130° 00'
127° 30'
125° 00'
122° 30'
>0.13
0.16
0.19
0.13
>0.16
0.10
<0.10
>0.10
0.10
>0.16
0.13
0.13
<0.07
0.07
<0.04
0.10
>0.10
>0.16
0.13
0.10
0.07
>0.16

FIG. 3. Plot of extinction coefficients calculated from data obtained during a quasisynoptic northeastern Pacific Ocean albacore survey along the west coast of North America.

is presumably within the area of influence of river discharge. Equally high values to the northwest are in the area of the turbid subarctic water and low values to the southwest are in the relatively clear subtropical water. Observations shown in Fig. 3 are supported by other data such as temperature, salinity, thermocline depth, and relative currents.

In the central North Pacific Ocean there is no upwelling[1] and no large river discharge comparable to those found along the west coast of North America. A major current system is present resulting from the eastward mixing of the cold Oyashio and warm Kuroshio currents. A broad transition zone is produced by the mixing of the currents ranging from clear blue subtropical water in the south to turbid green subarctic water to the north. A distinctive feature of this area is the northward progression of vernal warming accompanied by a large "wave" of standing crop of zooplankton (McGary, Graham, and Otsu 1958). This seasonal warming produced sharp thermoclines and shallow surface layers during the summer Cruise 32 of the *Manning* so that at times the thermocline reached the surface. In locations of these shallow surface layers and sharp thermoclines, extinction coefficients were high and sometimes exceeded the highest obtained along the west coast (Fig. 1).

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[1] Favorite et al. (1964) have obtained data implying a vertical movement towards the surface just south of the Aleutian Islands in the summer and spring.

In this regard, Murphy's (1959) correlation between extinction coefficients and ratios of surface troll to gill net catches of albacore tuna is of interest. The catches were made during *Manning* Cruise 32 and Cruise 36 (Table 1) in the central North Pacific Ocean and along the west coast, respectively. Data from the two cruises were segregated along his regression line so that those from the central North Pacific Ocean were associated with the above high extinction coefficients while those from along the west coast were associated with lower coefficients. Murphy attributed this difference to variations in fishing techniques between the two cruises. He also considered the sight of tuna in relation to turbidity and their ability to see fishing gear by using $1.7/\kappa$ as a first approximation of visual range. Considerations beyond a first approximation are limited, because there is no simple conversion between Secchi disc data and the sighting ranges of other objects (Duntley 1962). Also, there are possible differences in the optical conditions of the two areas, as indicated in Fig. 2.

The differences between intercepts and slopes of the regression lines in Fig. 2 are not entirely unexpected. The ratio $1.7/SD$ was determined originally for blue light. Although this relationship is correlated with red light (Riley 1956) and presumably other colors, the nature of the correlations might not be similar. Thus, one group of data could unduly influence another if it were combined with measurements from a surface water type having different spectral transmittance qualities. A significant regression line between the two groups could be obtained by adequately sampling their transition zone or area of mixing. The intercept of such a line would be the result of the combined data and would not necessarily pass through the origin.

In conclusion, the Secchi disc is a useful tool and the excellent agreement between disc observations and extinction coefficients is surprising considering the subjectivity of the method. However, caution should be observed when extrapolating the relationship between Secchi disc observations and extinction coefficients from one oceanic environment to another.

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A NEW DEPRESSOR DESIGN

BY JOSEPH J. GRAHAM AND GEORGE B. VAUGHAN

A New Depressor Design

At the U.S. Bureau of Commercial Fisheries Biological Laboratory at Boothbay Harbor, Maine, we are studying the distribution and abundance of the early life history stages of herring, *Clupea harengus* (Linnaeus) in relation to variations in the environment. Sampling results indicated that larvae avoided the meter net used at the surface and the otter trawl used along the bottom (Graham and Boyar, in press). To overcome this problem, we developed the Boothbay depressor for use with sampling devices at all depths at speeds of 7.4 to 12 km/hr.

An opportunity to observe the depressor on the bottom was afforded by the U.S. Bureau of Commercial Fisheries Exploratory Fishing and Gear Research Base, Gloucester, Massachusetts, which supplied a sonic transducer and underwater television equipment operated by Mr. Leon French. A test of the depressor in midwater was made from the

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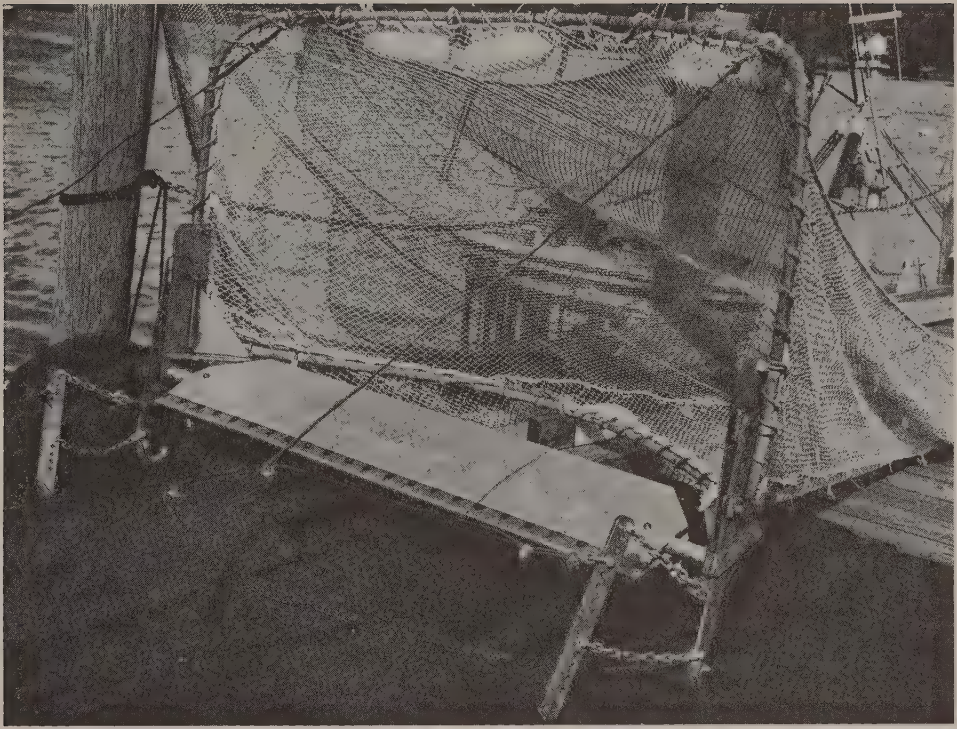
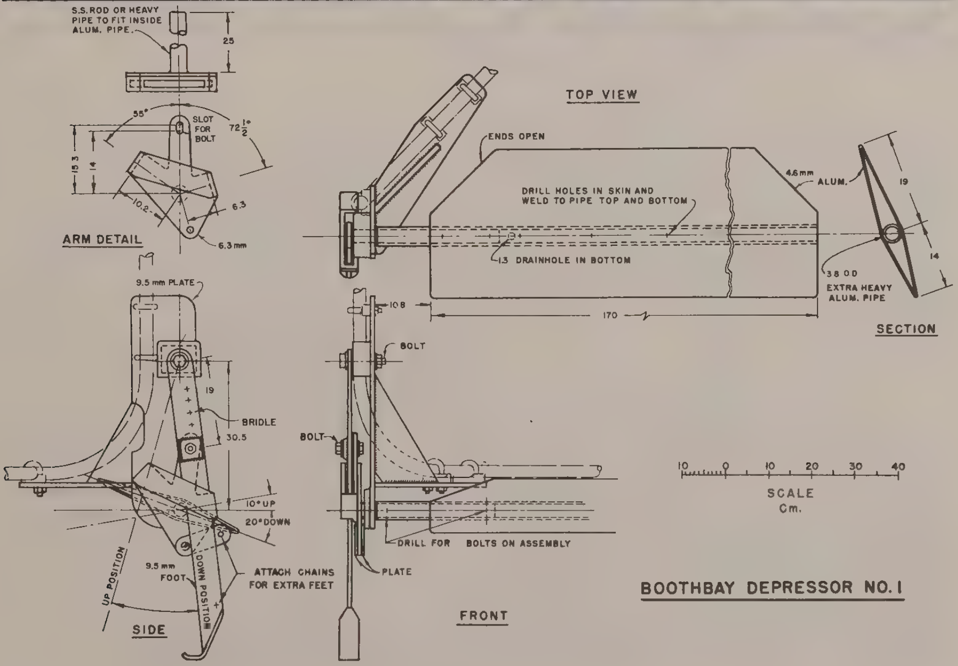
FIG. 1. Engineering drawing and photograph of Boothbay depressor No. 1 adapted to a trawl, 1 × 2-m opening.




S.S. ROD OR HEAVY PIPE TO FIT INSIDE ALUM. PIPE.
25
55°
SLOT FOR BOLT
72½°
15.3
14
10.2
6.3
6.3 mm
ARM DETAIL
9.5 mm PLATE
19
BRIDLE
30.5
10° UP
20° DOWN
9.5 mm FOOT
DOWN POSITION
UP POSITION
ATTACH CHAINS FOR EXTRA FEET
SIDE
TOP VIEW
ENDS OPEN
DRILL HOLES IN SKIN AND WELD TO PIPE TOP AND BOTTOM
4.6 mm ALUM.
13 DRAINHOLE IN BOTTOM
10.8
170
19
14
38 OD EXTRA HEAVY ALUM. PIPE
SECTION
BOLT
BOLT
DRILL FOR BOLTS ON ASSEMBLY
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FRONT
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SCALE Cm.
BOOTHBAY DEPRESSOR NO. I

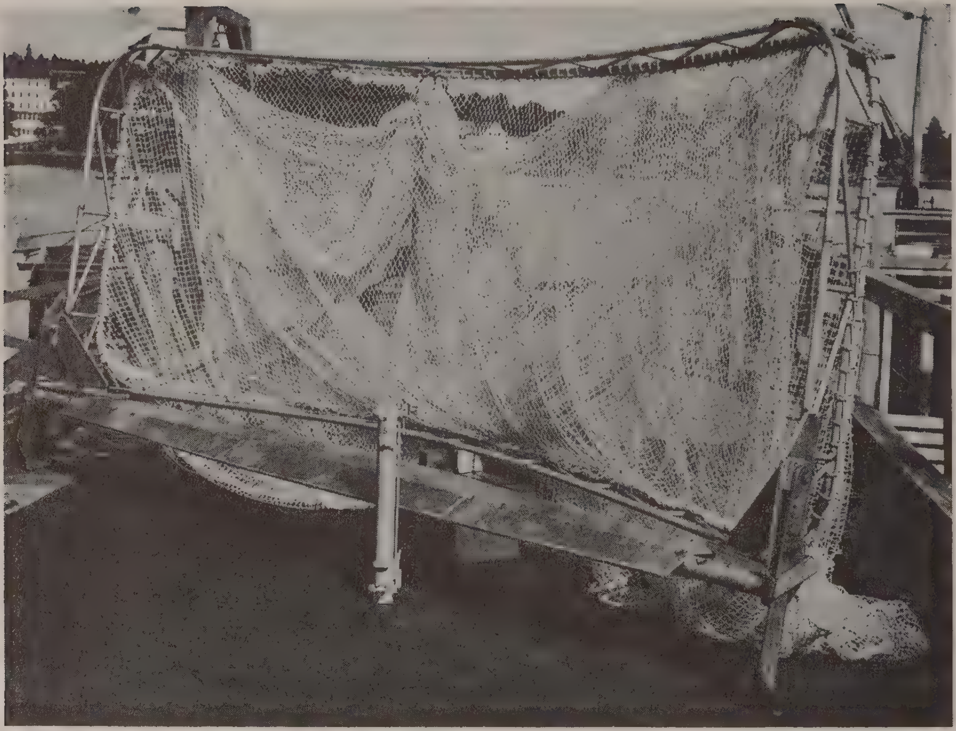

FIG. 2. Boothbay depressor No. 2 adapted to trawl, 1.5 × 4-m opening. Engineering drawings available on request. Nansen bottle included to indicate relative size.

MV Swan of the GM Defense Research Laboratories, Santa Barbara, California, with the assistance of Drs. William Aron and William D. Clarke under the auspices of the U.S. Office of Naval Research. The authors are especially indebted to Mr. Jack Gehringer for his encouragement and suggestions during development and testing of the design.

DESIGN AND OPERATION

The depressor, a pivoting blade (Fig. 1), is kept at a depressing angle (–20°) in midwater by the tension of the towing bridle. Upon bottom contact, pivoted feet, extending below the blade and connecting to it by arms, divert the blade from a depressing to a surfacing angle (+10°), thus preventing it from digging into the bottom. When the depressor rises from the bottom, tension from the bridle returns the blade to the depressing position.

Sensitivity of the depressor to bottom contact can be changed by altering the point of bridle attachment on the feet and thus the leverage on the blade. A series of holes in the feet is provided for shackling the bridle at different leverage points (Fig. 1). A chain may be stretched between the feet to provide additional force to the leverage system through bottom friction, and extra feet can be placed between the towing cable and the depressor to speed reaction of the depressor to contact with a rough bottom. This also lowers the attachment point of the bridle and further stabilizes the device. Depressing and surfacing angles and materials used in fabrication are a matter of design choice that depends upon requirements of a given sampling problem.

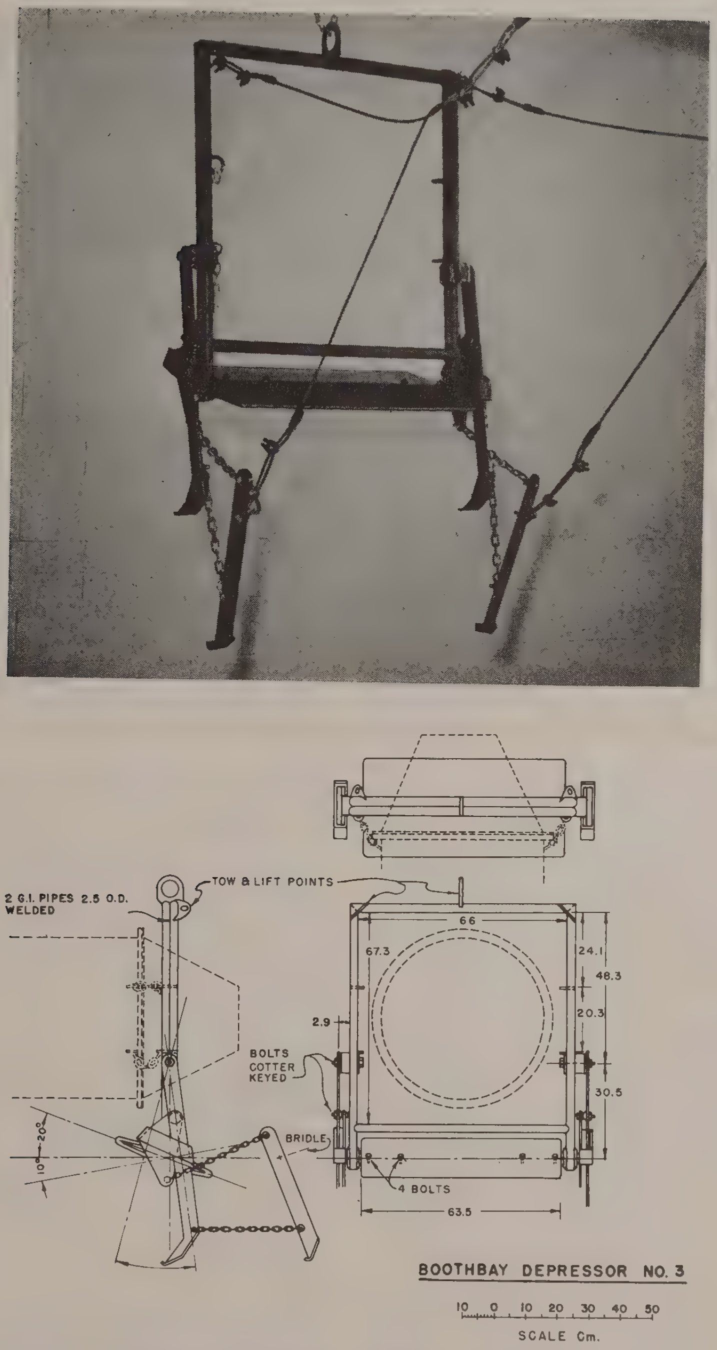
TOW & LIFT POINTS
2 G.I. PIPES 2.5 O.D. WELDED
66
67.3
24.1
48.3
20.3
2.9
BOLTS COTTER KEYED
30.5
BRIDLE
4 BOLTS
63.5
20°
10°
BOOTHBAY DEPRESSOR NO. 3
10 0 10 20 30 40 50
SCALE Cm.

FIG. 3. Engineering drawing and photograph of Boothbay depressor No. 3 adapted to a Gulf III sampler (indicated by dotted lines).

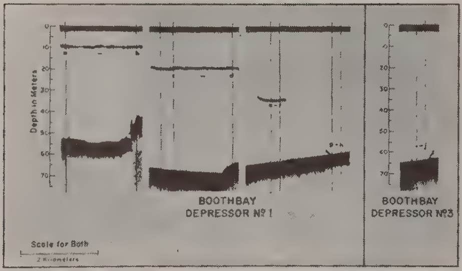

FIG. 4. Echo sounding record of depressors towed at 11.1 km/hr at various depths and on the bottom. No. 3 rose from the bottom when speed was increased to 13.3 km/hr (i–j). Direction of tow is to reader's right.

APPLICATION OF DESIGN

The Boothbay depressor No. 1 shown in Fig. 1 is bolted to a 1 × 2-m rectangular frame of galvanized pipe, 2.5 cm O.D., to which a trawl net is lashed. The addition of a stainless steel cap to the leading edge of the aluminum blade eliminates excessive damage when striking rock. The weight of the depressor alone is approximately 75 kg.

The Boothbay depressor No. 2 shown in Fig. 2 is welded to a 1.5 × 4-m frame of tubular aluminum. The light metal was used to facilitate transportation. This frame broke during television operations; it could not support the drag of the camera and light. The frame was replaced by galvanized pipe, 3.8 cm I.D., bolted to the depressor. The depressor, the pipe frame, and net are separated for truck transport. The weight of this depressor is approximately 100 kg.

The first two adaptations of the depressor design are intended for use with trawl nets and their towing characteristics depend partly upon the net design. The depressor in Fig. 3 is adapted to a standard gear, the Gulf III sampler, used to obtain fish larvae and plankton. The blade on the Boothbay depressor No. 3 is relatively small; its combined weight with the frame is 40 kg.

The stability of the Boothbay depressor No. 1 and trawl when towed at 11.1 km/hr through midwater and on the bottom is shown in Fig. 4. Bottom contact was maintained for at least 54 m. The data are from a sonic transducer, lashed to the trawl, which received its return signal from the water surface. The transducer was mounted on a board which acted as a drag requiring more wire out than usual to reach the depths towed. Therefore, the ratio of wire out-to-depth towed was determined by a bathythermograph attached to the trawl; this ratio was 3 : 1 in the shallow waters (10 to 90 m) usually fished.

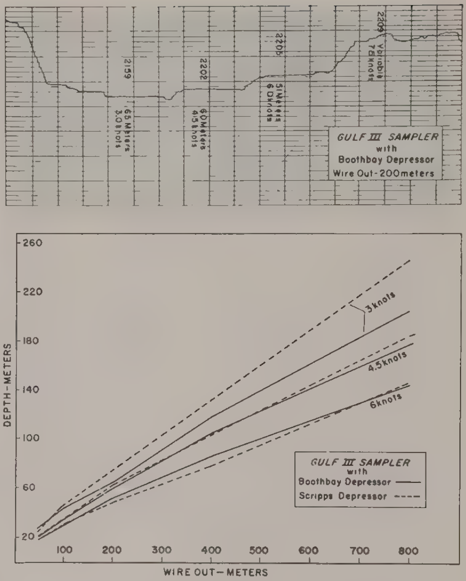

FIG. 5. Stability tests of Boothbay No. 3, and Scripps depressors with Gulf III attached. Upper panel is a record of a tow with 200 m of wire. The lower panel shows depths towed using 50, 100, 200, 400, and 800 m of wire.

The ratio of wire out-to-depth towed in midwater for the Boothbay depressor No. 2 and trawl was established at 8.3 km/hr as 3.5 : 1 by lashing a bathythermograph to the frame. On the bottom, the action of the trawl was observed on closed circuit television as it was towed at depths of 15 to 20 m. A line was attached to the center of the top span of the frame and a television camera and light on a trolley were lowered to within 1 to 3 m of the blade. The trawl moved over the bottom with only occasional interruptions, a barely discernible flick of the depressor blade, and a slight bounce. During the tow, the vessel passed over a rocky intrusion in the sandy bottom. The intrusion was 2 m high, approximately 80 m long, and covered with seaweed. As the trawl entered the weed, the depressor blade deflected upward a number of times until the crest was reached where a deflection of the full +10° raised the trawl over the crest. Smaller deflections continued as the trawl descended the other side.

The stability of the Boothbay depressor No. 3 in midwater was compared with that of the Scripps or Isaacs-Kidd Kite depressor when attached to the Gulf III sampler. The data were obtained in the coastal waters off Santa Barbara, California, using the General Motors research vessel *Swan* and the underwater electronics previously described by Aron et al. (1964). The depth of the gear was recorded as a trace (Fig. 5, upper panel) with stability indicated as a plateau. The steplike quality of the trace resulted from a slight hysteresis inherent in the mechanism recording the change in depth of the gear. A graph was prepared from the recorded data relating the depth towed to the amount of wire out (Fig. 5, lower panel). The two depressors towed at approximately the same depths at the higher speeds, 8.3 to 11.1 km/hr. Slight differences between them were related to departures of 0.18 to 0.37 km/hr from the selected towing speeds. The Boothbay depressor was unstable at 12 km/hr when it was towed with less than 50 m of wire out and was unstable at 13.9 km/hr with 400 m or less of wire out.

Bottom contact by the Boothbay depressor No. 3, with the Gulf III sampler attached, is shown in Fig. 4. The depressor made contact at 11.1 km/hr, was towed along the bottom, and then the towing speed was increased to 13.3 km/hr and the gear ascended.

DISCUSSION

The Boothbay depressors and their attached gears are used routinely to sample early life history stages of herring, and some results of these operations have been described (U.S. Fish and Wildlife Service 1965). Tows are made at selected stations from the bottom to the surface over a period of 30 min and at 7.4 to 12 km/hr depending upon the size of the gear towed. Rocky bottoms are sometimes sampled, but generally they are avoided because they portend the precipitous ledges common to the coastal area of the Gulf of Maine.

While the Boothbay depressor was developed to help solve problems in the distribution and abundance of the early life history stages of herring, it alleviates partly the general need for effective depressors (Gehringer 1962) for sampling from the surface to just above the bottom with a single gear.

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Biological Laboratory,
Boothbay Harbor, Maine 04538.

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Sea Frontiers

Magazine of the INTERNATIONAL OCEANOGRAPHIC FOUNDATION

Balloons for Storm Observations

[illegible]

Volume 12, No. 3 May-June, 1966

Balloons for Marine Observations

By ROGER E. GREEN
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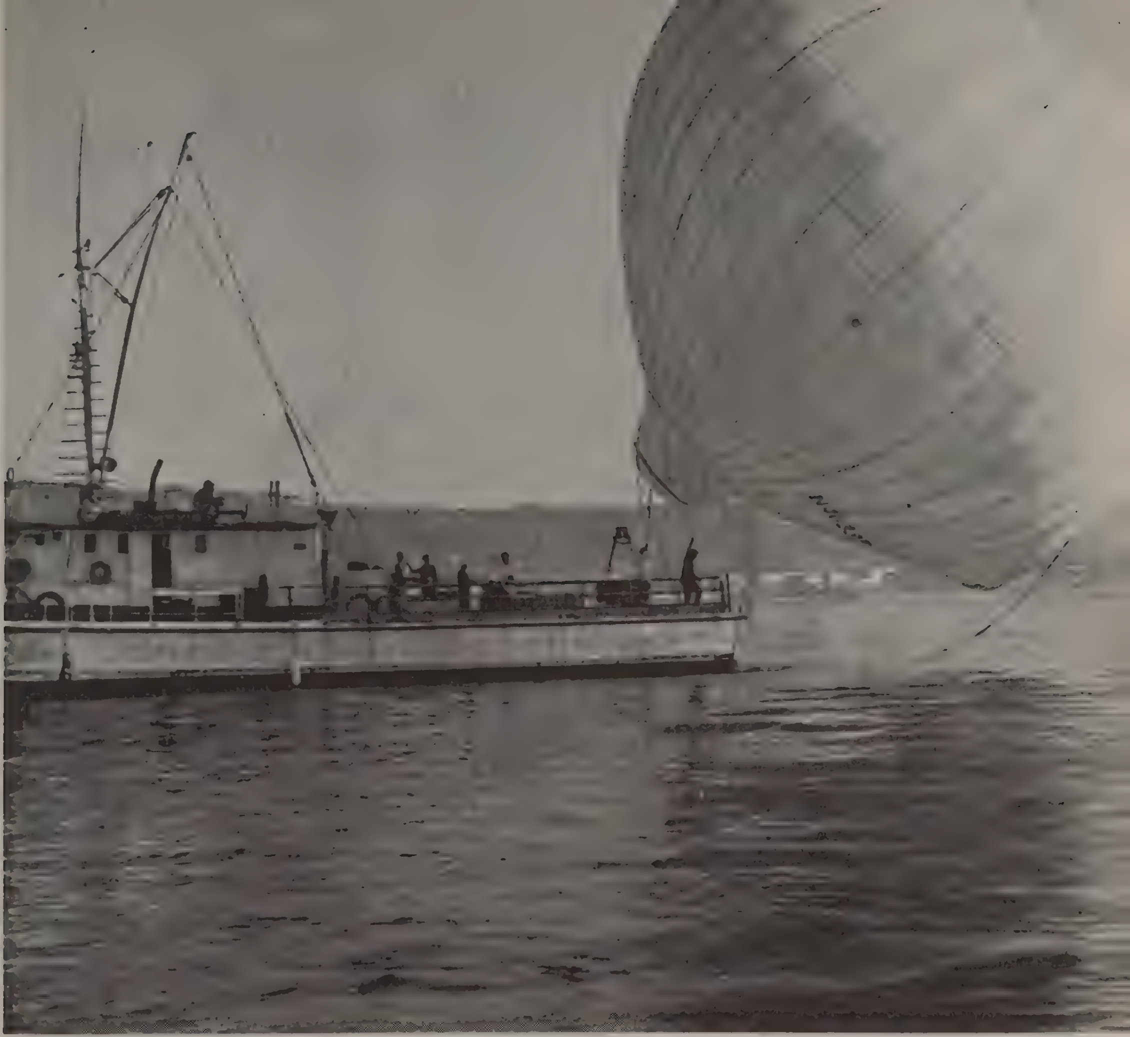
Tuna Resources Laboratory
La Jolla, California

THE OLDEST type of flying machine, the hot-air balloon, first made men airbone in 1783 when an ascent was made by the Montgolfier brothers of France. But the development of lighter-than-air craft long ago became overshadowed by rapid break-throughs in the development of heavier-than-air craft. Nevertheless, the unique advantages of the former are now finding more and more scientific applications even as the age of outer space begins. Some of these applications may be found in communications, meteorology, atmospheric research, astronomy, and recovery systems. The most recent of these is the use of balloons in the fishery and oceanographic sciences.

In 1965 the Bureau of Commercial Fisheries Tuna Resources Laboratory at La Jolla, California, tested the use of lighter-than-air vehicles for spotting purposes in commercial fishing and marine research. We sought an inexpensive substitute for airplanes—something which could operate from fishing vessels and research ships independently of shore-based facilities.



GOING UP! *Hot air balloon tethered to the M/V* Yaqui Queen *proved possible use for spotting and observing fishes and other marine animals. (Roger E. Green)*

No hot-air balloon has been designed and built for both operating at sea and towing in windy conditions. Part of our purpose, therefore, was to develop design ideas as we tested balloons. A hot-air balloon supplied by Litton Systems, Inc., was used in the first experiment.

The tests took place 4 miles off La Jolla from the M/V *Yaqui Queen*. The spherical dacron balloon, about 50 feet in diameter, supported a tubular, aluminum-frame gondola that could hold two persons. A ducted fan driven by a ¼-horsepower electric motor mounted at the base of the balloon provided inflation and maintenance of an internal pressure of about 2 pounds per square foot. Air in the balloon was heated by a propane burner mounted in the base of the balloon and supplied by a hose to a pressurized propane tank mounted on the deck of the ship. Extra pressure was supplied by a 50-pound cylinder of inert gas that forced the liquified propane to a height of 500 feet. A hydraulic winch was used to handle a ⅝-inch nylon line which tethered the balloon to the ship.

Inflation of the balloon was accomplished easily in about half an hour while trailing the deflated balloon on the sea surface off the stern of the boat. The balloon was deflated by activating a release device at the top of the balloon which held four zippers shut. When the zippers were released the top of the bag opened and the hot air escaped rapidly.

Airborne on Hot Air

Four manned and two unmanned ascensions of the balloon were made in a variety of weather and sea conditions, ranging from dead calm to winds of 12 knots with moderate seas.

In calm weather, five ascents were made up to 500 feet. Total air time was approximately 8 hours. All personnel who made ascensions were impressed with the exceptional stability of the balloon, cushioned against the rolls of the ship by its long tethering line. Binoculars and cameras with telephoto lenses could be used without the stabilizing devices commonly required in aircraft. Vertical movements of the balloon were accomplished easily by burner adjustments made either at the gondola or at the propane tank on the ship. Controlled "touch and go" landings on the water were possible by adjustment of the burner.

LIFTING, KITE-LIKE EFFECT *is achieved with a Vee-Line helium-filled balloon. This shape allows towing without hampering speed or maneuverability of vessel. (Roger E. Green)*

Hot-Air Versus Helium

One of the advantages of hot air over helium is its tolerance to holes in the balloon fabric. After one inflation, the balloon swayed against a boat railing which caught one of the balloon's guy-lines. On the opposite roll, a rip started in the material and extended from the bottom of the balloon to midway up the side (the material was not provided with rip stops). Even with this extensive rent, the balloon retained its hot air and its shape for another 15 or 20 minutes. Had the rent occurred while the balloon was manned and airborne, sufficient lift would have been retained to allow a safe descent. Repairs were made easily with a portable sewing machine.

Maneuvers were made to observe the effect of severe strains on the balloon. Because the balloon was spherical it had a theoretical limitation of 5 knots relative air velocity. When tested in a 24-knot wind (accomplished by turning the boat, moving at 12 knots, into a 12-knot wind) the balloon was forced down to the water's surface — but only after the burner flame was reduced.

DART
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The shifting of the air mass inside the balloon caused a rupture in the fabric as it hit the water and it rebounded before it finally settled on the surface. The descent was slow — much slower than that of a parachute. If the balloon had been manned, the occupant would have been in little danger aside from a brief wetting.

Unmanned Helium Balloon Test

Tests with the hot-air balloon proved that a spherical shape has severe limitations in towing and in high winds. With this in mind, we made a test October 29, 1965, of a small unmanned model of an aerodynamically shaped balloon manufactured by Vee-Line Company of Compton, California. The small size of the balloon (200 cubic feet), and the use of helium, did not detract from the value of observations of its flight characteristics. This test showed that a satisfactory aerodynamic shape of the balloon, designed to increase its lift in a wind or when moving, could be achieved which allowed towing without hampering the speed or maneuverability of the vessel.

Two experiments were conducted to take full advantage of the limited payload of the small balloon. In one, a simple, fixed-focus camera with motorized film advance and automatic iris was linked to servo equipment that operated its shutter on command from a radio-control transmitter. Pictures were thus obtained of the vessel and the sea surface from altitudes of 100-500 feet. This setup might be useful for observations of the behavior of fish schools and marine mammals.

The second experiment concerned the possible use of small, unmanned balloons as "aerial-moored buoys" to obtain various air-sea interface measurements. Many of these oceanographic observations, at present, suffer from the so-called "investigator effect" caused by the proximity of the ship or other platform from which the observations are made, and also from inability to measure interaction at close and constant distances above the actual sea surface. These measurements might be made by sensors on lines supported by a suitably moored balloon, thereby approximating open-sea conditions. We found that suitable mooring could be obtained with a sea anchor suspended just below the surface of the water. So little of this mooring broke the sea surface that little "investigator effect" is anticipated from the mooring systems.

The Advantages of Height

The advantages of height are well known to fishermen. On fishing boats one or more lookouts are often placed as high as possible to spot fish and to maneuver the boat to aid in their capture. To gain the advantages of increased height, the use of aircraft has developed rapidly in the U.S. tuna fishing fleet. Seaplanes and helicopters, operated from fishing vessels, and land-based airplanes have been tried by the tuna fleet. The former two were impractical because of difficulties of maintenance and operation at sea. Land-based aircraft

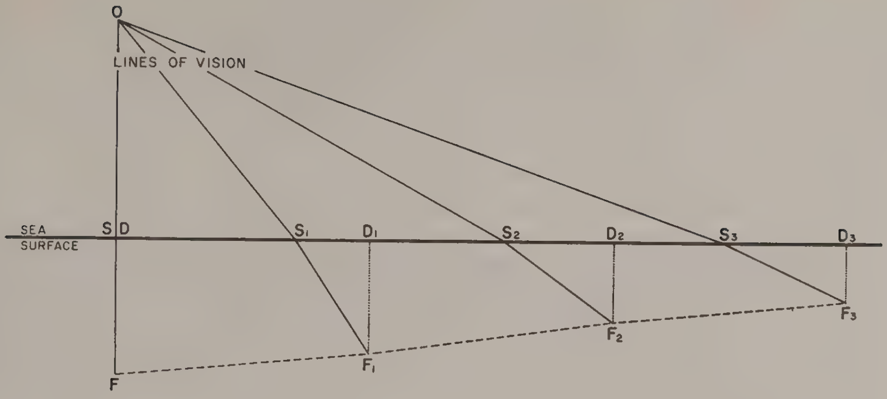
O
LINES OF VISION
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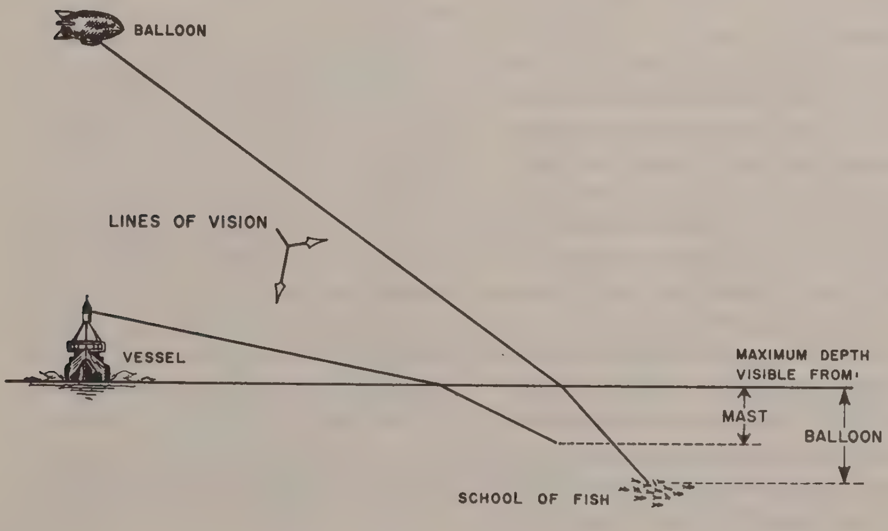
DIAGRAM ABOVE *shows the maximum depths of visibility below the surface at different lateral distances from an observer above the water. At all angles the length of visibility through the water, S to F (a measure of the transparency of the water), remains the same; but when the lateral distance increases, the depth into the water, D to F, becomes less. Thus, a balloon observer can see deeper into the water than can a lookout on a ship.*

MORE DIRECT UNDERWATER PATH *of vision from the balloon to the school of fish enables an observer in a balloon to see the school at a greater depth. He is thus in a better position to observe fish behavior or to direct the setting of the purse seine.*


BALLOON
LINES OF VISION
VESSEL
MAXIMUM DEPTH
VISIBLE FROM
MAST
BALLOON
SCHOOL OF FISH

continue to be important to the fleet in areas where landing strips are located near the fishing grounds. In 1963, about 8 per cent of the total U.S. tropical tuna landings were made with the assistance of aircraft. Airplanes are so valuable for this purpose that boat owners pay 5 per cent or more of the gross value of fish caught for aerial assistance.

Directing the maneuvering of a boat around a school of fish is more easily achieved from a plane than from the ship because the observer at higher altitude can see deeper into the water for reasons related to the water transparency and the length of the refracted line of vision through the water. The observer at heights can also scan a wider expanse of water. Under ideal atmospheric conditions, it is theoretically possible to see surface objects as far away as the horizon. In practice, the maximum distance to which an object at the surface is seen depends on such things as the surface disturbance it creates, haze, and the optical system used. For an observer at a 600-foot altitude, the horizon is 30 miles away, whereas, for an observer in a crow's nest at 60 feet, the horizon is at 9.5 miles. At a particular location, then, the area circumscribed by the horizon is ten times as great from an altitude of 600 feet as it is from 60 feet. The observer in a balloon at 600 feet could scan over three times as great a distance along a cruise track. The area scanned along the path of a 1,000-mile track, from that altitude, would be about 60,000 square miles compared with about 19,000 square miles which could be observed from a crow's nest.

Height is advantageous for many types of scientific marine observations. A stable platform capable of operating and hovering at low altitudes would be useful for quantitative studies of individual fish movements involved in schooling. A laboratory phase of these studies is in progress at present at the Tuna Resources Laboratory. A balloon towed by a research vessel on an oceanographic cruise track would extend visual coverage of the water for fish schools or porpoises by thousands of square miles. Certain oceanographic measurements in the boundary layer, such as profiles of air mass, wind, salt, humidity, temperature, measurements of incoming and back radiation, could be made advantageously at height.

What's In the Wind

The tests indicate that operation of ship-based balloons is feasible, especially if a balloon is designed specifically for this purpose. The problems of towing a balloon under windy conditions can be solved with a balloon designed to give a lifting, kite-like action. The balloon can withstand considerable ship's roll if tethered with a long resilient cable as near amidship as possible. For heavy seas, a section of shock-absorbing line could be inserted. Operating height is limited only by the fuel-delivery system. No problem was encountered in supplying fuel to 500 feet, nor is any anticipated in operating to 1,000 feet. There is no advantage in operating at a higher al-

TOUCH-AND-GO LANDING *of hot-air balloon is made on the sea surface. Inner tube flotation attached to the gondola is a safety precaution. Aloft, the balloon was reported to have exceptional stability. Binoculars and cameras were used without the stabilizing devices commonly required in aircraft. (Roger E. Green)*

titude. Compared to other types of aircraft, the hot-air balloon is cheapest, simplest to operate, and probably the safest. No difficult pilot skills or license requirements are needed to operate a balloon. The balloon offers the advantage of being able to "hover" over an area at any desirable height. The attachment to the ship offers advantages for directing the setting of seines since the observer is always in an advantageous position above the school. Its chief disadvantage is its immobility; it moves only with the ship. Balloons might, therefore, have some limitation as fish-scouting vehicles.

Helium is not presently being considered for manned balloons at sea due to its cost, bulky storage, and the serious consequences of even small leaks in the balloon fabric. It may be useful, however, for smaller, unmanned systems.

The Bureau has plans for further investigations of both scientific and fishing uses for balloons. At some time in the future, it may not seem strange to see these unique craft in the service of American fishermen.

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REVISION OF THE FLOUNDER GENUS *ANCYLOPSETTA* (HETEROSOMATA: BOTHIDAE) WITH DESCRIPTIONS OF TWO NEW SPECIES FROM THE ANTILLES AND THE CARIBBEAN SEA[1]

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ABSTRACT

Ancylopsetta antillarum and *A. microctenus* are described as new species of flatfishes. A diagnosis, brief description, relationships, range, and illustration are provided for each species of *Ancylopsetta* and the monotypic *Gastropsetta*. The two new species are distinguished from the other five *Ancylopsetta* by the relative length of the first 5 dorsal-fin rays (first 2 rays short, next 2 or 3 elongate) and from each other by the degree of development of ctenii on the scales of the ocular side. Known ranges are extended for *A. cycloidea, A. dilecta, A. kumperae,* and *Gastropsetta frontalis*. A key is included for identifying the species of *Ancylopsetta* and *Gastropsetta.*

INTRODUCTION AND ACKNOWLEDGMENTS

Two new species of *Ancylopsetta* (Heterosomata: Bothidae) have been collected in the Antilles and the Caribbean Sea on cruises of the U. S. Bureau of Commercial Fisheries exploratory fishing vessels SILVER BAY and OREGON. When Norman (1934) revised the family Bothidae, *Ancylopsetta* was represented by *A. dilecta* (Goode & Bean, 1883), *A. dendritica* Gilbert 1890, and *A. quadrocellata* Gill 1864. Tyler (1959) described *A. cycloidea* and *A. kumperae*. The addition of the two new species described here increases the number of known species to seven. Five of these have three prominent ocellated spots on the ocular side of the body, and *A. quadrocellata* and *A. kumperae* have four. Six species occur in the Atlantic Ocean, Gulf of Mexico, and Caribbean Sea, ranging from North Carolina to northern Brazil in depths of 2 to 250 fathoms (Fig. 6). The single Pacific species, *A. dendritica,* ranges from the Gulf of California to Ecuador in about 11-27 fathoms.

For the loan of, and information on, specimens, I thank James E. Böhlke and James C. Tyler, Academy of Natural Sciences of Philadelphia; John C. Briggs, University of South Florida; Milton J. Lindner and Donald Moore, U. S. Bureau of Commercial Fisheries Biological Laboratory, Galveston, Texas; C. Richard Robins, Institute of Marine Science, University of Miami; Leonard P. Schultz, U. S. National Museum; Royal D. Suttkus,

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[1] Contribution No. 80, U. S. Bureau of Commercial Fisheries Biological Laboratory, Brunswick, Georgia.

TABLE 1

Ancylopsetta antillarum—SELECTED MEASUREMENTS (IN PER CENT OF STANDARD LENGTH AND HEAD LENGTH) AND COUNTS FOR THE HOLOTYPE* AND PARATYPES

	Standard length in mm	49	74	81	98	111	114	132	135	136	146	152	163	178	195
Per cent SL	Head length	33	31	31	32	31	31	28	31	29	29	29	28	30	28
	Longest dorsal-fin ray	47	36	36	45	35	32	[1]	33	35	29	35	28	32	29
	Length pelvic fin ocular side	38	39	44	42	36	31	28	31	35	33	27	28	35	27
	Body depth	48	51	51	46	50	48	50	50	50	48	50	53	49	49
	Head length in mm	16	23	25	31	34	35	36	42	40	43	44	45	52	54
Per cent HL	Length first dorsal-fin ray	26	30	30	31	33	30	30	24	31	28	28	31	30	25
	Length second dorsal-fin ray	56	46	46	60	54	53	48	39	45	51	45	52	45	42
	Length third dorsal-fin ray	143	101	[1]	144	110	106	[1]	100	116	96	112	101	94	77
	Length fourth dorsal-fin ray	130	114	127	135	113	100	93	107	119	94	116	99	108	97
	Length fifth dorsal-fin ray	99	61	94	124	97	90	55	60	75	54	95	76	70	70
Counts	DFR ant. cent. of D. Oc.[2]	31	29	32	33	29	33	32	30	34	31	31	32	33	31
	DFR pos. cent. of D. Oc.[3]	36	37	37	37	33	34	33	34	35	35	34	36	39	35
	AFR ant. cent. of V. Oc.[4]	18	19	19	19	19	20	21	20	20	19	19	19	19	21
	AFR pos. cent. of V. Oc.[5]	33	34	35	35	32	32	32	28	33	35	33	36	25	33
	Dorsal-fin rays	67	66	69	70	62	67	65	64	69	66	65	68	72	66
	Anal-fin rays	51	53	54	54	51	52	53	48	53	54	52	55	54	54
	Scales on lateral line	71	72	72	71	73	71	75	71	73	77	70	74	77	79

Tulane University; and Loren P. Woods and Pearl Sonoda, Chicago Natural History Museum.

For reviewing the manuscript and offering many helpful suggestions I thank William W. Anderson, Jack W. Gehringer, and William D. Anderson, Jr., Bureau of Commercial Fisheries Biological Laboratory, Brunswick, Georgia; Frederick H. Berry, Bureau of Commercial Fisheries Tropical Atlantic Biological Laboratory, Miami, Florida; Earl E. Deubler, Jr., University of North Carolina; Carter R. Gilbert, University of Florida; John E. Fitch, California Department of Fish and Game; and James C. Tyler, Academy of Natural Sciences of Philadelphia. The illustrations were prepared by Grady W. Reinert.

The following abbreviations are used to designate the museums from which specimens were examined: ANSP, Academy of Natural Sciences of Philadelphia; BLBG, U. S. Bureau of Commercial Fisheries Biological Laboratory, Brunswick, Georgia; BMNH, British Museum (Natural History); CNHM, Chicago Natural History Museum; MCZ, Museum of Comparative Zoology, Harvard College; SU, Stanford University; TABL,

TABLE 1 (Continued)

	Standard length in mm	203	216	220	230	230	231	232	235	238	255	265	282	290	296*
Per cent SL	Head length	30	28	29	28	29	28	29	27	27	30	28	29	28	30
	Longest dorsal-fin ray	26	27	15	17	18	25	[1]	20	14	18	18	13	[1]	14
	Length pelvic fin ocular side	32	[1]	25	26	23	27	26	21	19	22	25	20	19	18
	Body depth	55	51	50	49	51	50	52	49	50	54	51	50	48	52
	Head length in mm	61	61	63	64	66	65	66	64	65	75	75	82	82	88
Per cent HL	Length first dorsal-fin ray	25	26	26	26	24	26	25	23	27	22	25	26	22	21
	Length second dorsal-fin ray	34	42	48	37	40	39	37	35	44	32	35	34	38	31
	Length third dorsal-fin ray	85	91	[1]	60	63	86	[1]	69	49	47	63	[1]	[1]	48
	Length fourth dorsal-fin ray	67	68	50	52	62	63	[1]	60	52	60	51	[1]	[1]	[1]
	Length fifth dorsal-fin ray	52	60	53	51	49	43	48	48	49	43	42	46	36	40
Counts	DFR ant. cent. of D. Oc.[2]	32	32	32	31	31	30	31	31	32	33	30	33	31	33
	DFR pos. cent. of D. Oc.[3]	37	35	36	35	38	35	35	35	33	38	36	37	37	34
	AFR ant. cent. of V. Oc.[4]	19	19	19	18	22	19	20	20	20	22	20	20	21	19
	AFR pos. cent. of V. Oc.[5]	34	34	33	34	34	34	31	32	33	34	33	33	33	34
	Dorsal-fin rays	69	67	68	66	69	65	66	66	65	71	66	70	68	67
	Anal-fin rays	53	53	52	52	56	53	51	52	53	56	53	53	54	53
	Scales on lateral line	78	75	75	76	74	76	74	73	78	77	78	80	77	79

[1] = Broken.
[2] = DFR ant. cent. of D. Oc. = Number of dorsal-fin rays anterior to a vertical midline of the dorsal ocellus.
[3] = DFR pos. cent. of D. Oc. = Number of dorsal-fin rays posterior to a vertical midline of the dorsal ocellus.
[4] = AFR ant. cent. of V. Oc. = Number of anal-fin rays anterior to a vertical midline of the ventral ocellus
[5] = AFR pos. cent. of V. Oc. = Number of anal-fin rays posterior to a vertical midline of the ventral ocellus

U. S. Bureau of Commercial Fisheries Tropical Atlantic Biological Laboratory, Miami, Florida; TU, Tulane University; UMML, University of Miami, Marine Laboratory; USNM, United States National Museum.

METHODS

All measurements were taken with a dial caliper and recorded to the nearest tenth millimeter except for standard and total lengths on specimens exceeding 200 mm, which were measured with a millimeter rule. Measurements were taken on ocular side of body unless otherwise stated. Proportional measurements in the text are given as range in percentage of standard length or head length.

Standard length—Tip of snout to end of hypural plate, on blind side.
Total length—Tip of snout to end of longest caudal-fin ray, on blind side.
Head length—Tip of snout to posteromost point on fleshy margin of opercle.
Body depth—Greatest vertical measurement, excluding fin rays.

Eye diameter—Horizontal distance across eye, not a measurement of the orbit.

Pectoral-fin length—From base of first (anterior) pectoral ray to tip of longest ray.

Pelvic-fin length—From base of first pelvic ray to tip of longest ray.

Upper-jaw length—Anterior edge of premaxillary to posterior edge of maxillary.

Lower-jaw length—Symphysis of dentary to posterior edge of angular.

Snout length—Anteromost edge of upper jaw to anteromost edge of orbit of lower eye.

Snout to preopercle—Anteromost edge of upper jaw to posteromost edge of preopercle.

Dorsal-fin ray length—Base to tip of each fin ray, measured on ocular side where possible. (The length of some dorsal-fin rays could not be measured accurately because of their fragility or distortion after preservation.)

Dorsal-fin rays—Total number of rays (for all species), and number anterior to and number posterior to a vertical through center of dorsal ocellus (three-spotted Atlantic species only).

Anal-fin rays—Total number of rays, and number anterior to and number posterior to a vertical through center of ventral ocellus (as above).

Gillrakers—Total, lower limb, and upper limb; including rudiments.

Scales in lateral line—Number in lateral line from above point of connection of opercular membrane with body to end of hypural plate; counts recorded as total, curved portion, and straight portion. (On some specimens the junction of the curved and straight portions of lateral line cannot be precisely determined.)

Vertebrae—Abdominal and caudal. (The first caudal vertebra has its enlarged haemal spine in contact with the first and enlarged pterygiophore of the anal fin.)

Ancylopsetta Gill

Ancylopsetta Gill, 1864:224 (Type species *Ancylopsetta quadrocellata* Gill, 1864, by monotypy).

Notosema Goode & Bean, 1883:192 (Type species *Notosema dilecta* Goode & Bean, 1883, by monotypy).

Ramularia Jordan & Evermann, 1898:2633 (Type species *Ancylopsetta dendritica* Gilbert, 1890, by monotypy).

Sinistral, body ovate and compressed, greatest depth about ½ SL. Anterior profile of head concave anterior to upper eye. Eyes separated by a scaled, or naked, narrow ridge or flat space. Jaws and dentition about equally developed both sides; teeth uniserial both jaws, conical, small, increasing in size anteriorly; lower jaw included. Gillrakers elongate to short and broad. Tip of first interhaemal spine not projecting through skin in advance of anal fin. Lateral line well developed on both sides of body. Origin of dorsal fin above, slightly in advance of, or behind anterior margin of upper eye, commencing behind posterior nostril on blind side. Pectoral and pelvic fins of ocular side longer than on blind side; pelvic fin of ocular side elongate. Scales ctenoid on ocular side; ctenoid, cycloid, or both on blind side. Vent on blind side, above or in an anterolateral direction from origin of first anal-fin ray; posterior edge of pelvic fin on blind side not attached to membrane adjacent to vent. Urogenital pore on ocular side, opposite vent. Urohyal with a well-developed keel on its anteroventrally directed arm; width of keel on lower portion of arm 2-3 times greater than diameter of shaft from which it projects.

Seven species, all in the new world.

Ancylopsetta antillarum, new species

Fig. 1; Tables 1, 3, and 4

Diagnosis.—An *Ancylopsetta* with three ocellated spots on ocular side. Scales of ocular side with well-developed ctenii projecting beyond scale margin. First and 2nd rays of dorsal fin short; 3rd, 4th, and 5th rays long; 6th shorter and about as long as succeeding rays; on some large specimens 3rd, 4th, and 5th dorsal-fin rays only slightly longer than succeeding rays. Dorsal-fin rays anterior to a vertical through center of dorsal ocellus 29-34. Blind side dusky, becoming less noticeable on some large specimens.

Description.—Counts and measurements of selected characters of the holotype and 27 paratypes are shown in Table 1, and other counts and measurements in Tables 3 and 4. Additional measurements discussed in he text were taken on all specimens but are not shown in Tables 1, 3, or 4. Range of characters in the text is followed by the value for the holotype in parentheses.

Head length 27-33 (30) per cent SL. Diameter of upper eye 7-12 (12) per cent SL and 25-38 (25) per cent HL, about equal to lower eye (eyes distended and distorted on some specimens brought up from great depths). Snout length 19-21 (20) per cent HL. Snout to preopercle distance 76-82 (78) per cent HL. Upper jaw length 42-47 (43) per cent HL. Lower jaw length 50-58 (50) per cent HL. Body depth 46-55 (52) per cent SL.

Dorsal-fin rays total 62-72 (67), anterior to a vertical through center of dorsal ocellus 29-34 (33), posterior to the vertical 33-39 (34). Longest dorsal-fin ray 13-47 (14) per cent SL, longest anterior dorsal-fin ray usually slightly longer than or nearly equal to head length in specimens smaller than about 200 mm SL, becoming progressively shorter at sizes larger than about 200 mm SL (Fig. 5). Length of 1st ray 21-33 (21) per

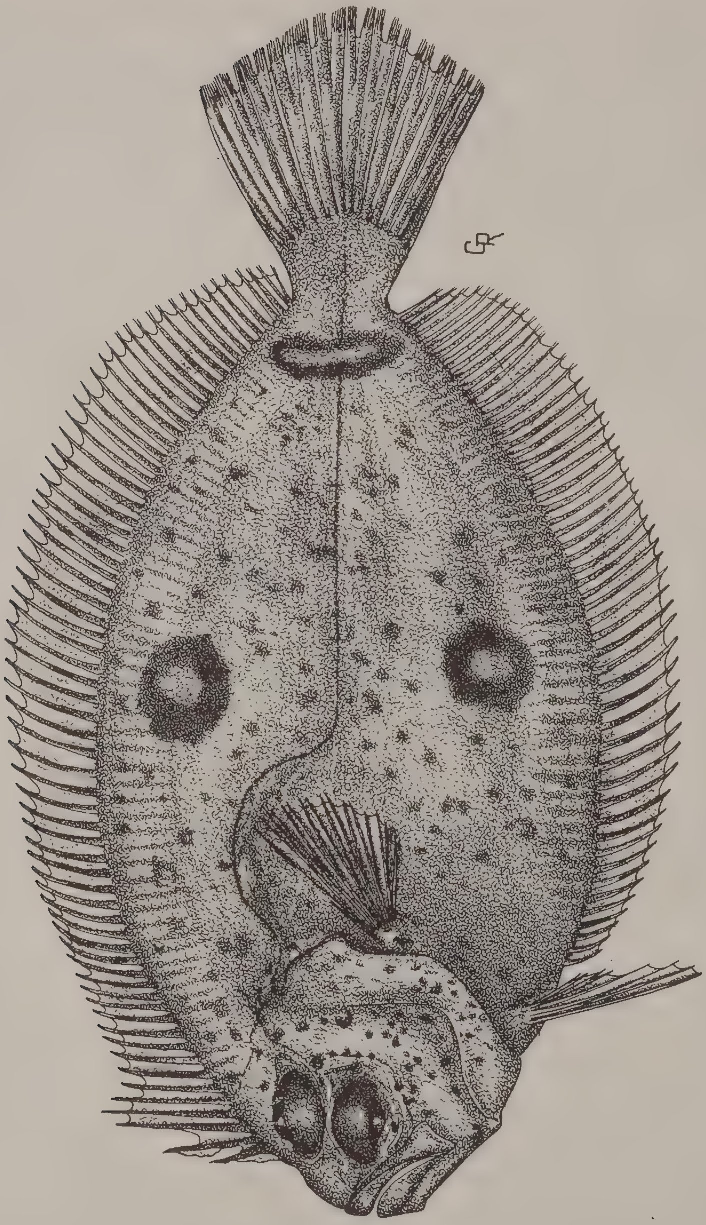

FIGURE 1. Holotype *Ancylopsetta antillarum.*

cent HL, 2nd ray 31-60 (31) per cent HL, 3rd ray 47-144 (48) per cent HL, 4th ray 50-135 (broken) per cent HL, 5th ray 36-124 (40) per cent HL.

Anal-fin rays total 48-56 (53), anterior to a vertical through center of ventral ocellus 18-22 (19), posterior to vertical 28-36 (34).

Pectoral-fin rays ocular side 9-12 (10), two most dorsal rays and most ventral ray unbranched, others branched; rays blind side 9-11 (10). Pectoral-fin length ocular side 15-24 (18) per cent SL; length blind side 12-15 (12) per cent SL.

Pelvic-fin rays 6 (6). Pelvic-fin length ocular side 18-44 (18) per cent SL, usually 2½ times (or more) length of pelvic fin on blind side on specimens smaller than about 200 mm SL, and less than 2½ times that of blind side in larger specimens. Pelvic-fin length blind side 9-13 (11) per cent SL. Longest pelvic-fin ray of ocular side longer than head to about 150 mm SL, either longer or shorter than head between 150 and 210 mm SL, and shorter than head above about 210 mm SL. Shape of pelvic fin on ocular side variable: the 1st, 2nd, or 3rd ray longest (Figs. 1 and 5); several of the rays about equal (Figs. 5A, C and D); or length gradually reduced from first to last ray (Fig. 1).

Caudal-fin rays 17 (17); two outermost principal rays on dorsal and ventral edges unbranched, others branched.

Gillrakers, including rudiments, total 8-12 (10), lower limb 6-8 (7), upper limb 2-4 (3).

Vertebrae 10 + 25-27 (10 + 26).

Nostrils on ocular side anterior to lower eye and separated. Anterior nostrils elevated (less on blind side than on ocular side), flap on distal margin of anterior nostrils extending posteriorly (on some small specimens flap extends beyond posterior margin of posterior nostril), anterior nostrils smaller than posterior nostrils. Nostrils on blind side anterior to origin of dorsal fin. Nostrils with 20 lamellae arranged transversely around a median rachis.

Scales in lateral line total 70-80 (79), curved portion 26-32 (31), straight portion 42-49 (48). Scales of ocular side with strong, well-developed ctenii extending beyond posterior margin of scales (see Fig. 4). Ocular side covered with scales except for pectoral fin and base, upper and lower jaws, snout, interorbital ridge, branchiostegal membranes, interradial membranes of dorsal, anal, pelvic, and caudal fins, and small fleshy flap of skin on ventral surface of interopercle. Scales on blind side cycloid (on a few specimens ctenoid scales on ocular side of peduncle overlap onto blind side), deeply imbedded. Naked areas on blind side similar to those on ocular side.

Teeth uniserial, about equally developed both sides. Teeth in lower jaw slightly larger than or equal to those in upper jaw (anterior canines in lower jaw slightly smaller than those in upper jaw in some specimens). Teeth of upper jaw on anterior ¾ of premaxillary, decreasing in size posteriorly, several large canines present on anterior portion of premaxillary. Vomer, palatines, and tongue toothless. Pharyngeal teeth in three rows.

Three prominent ocellated spots on ocular side. Posterior spot generally rectangular, but may be oval, located on lateral line just anterior to caudal peduncle, dorsal and ventral margins extending almost to dorsal and anal fins respectively. Anterior two spots located just anterior to midpoint of body, one below the dorsal fin, the other above the anal fin (Fig. 1). On smallest specimen (49.2 mm SL) spots not ocellated, next largest (74.3 mm SL) the two anterior spots ocellated, by 98 mm SL all three ocellated. Pigmentation of ocellated spot variable but generally with the following basic pattern: pale center surrounded by darker area, darker area encompassed by narrow light area (difficult to discern in some specimens).

General body color ocular side (preserved material), dark brown or tan with numerous, irregularly spaced spots and blotches. Fin rays and inter-radial membranes on ocular side partially covered with melanophores, except inter-radial membranes of pectoral fin. Pelvic fin of ocular side and caudal fin more profusely pigmented than other fins. Dark spots and blotches on dorsal and anal fins. Pigmentation on ocular side sometimes extending onto blind side in some smaller specimens, but at no size is coloration on blind side as intense as on ocular side.

Blind side straw-colored and partially overlaid with melanophores, resulting in dusky appearance. Pectoral fin of blind side not pigmented. Membrane overlying pelvic, dorsal, anal, and caudal fin rays covered with melanophores, but inter-radial membranes of these fins usually clear.

Relationships.—*A. antillarum* is most closely related to *A. microctenus,* and next to *A. dilecta.* The shortened first two dorsal-fin rays (see Fig. 3), absence of prominent fleshy projections on tips of some anterior dorsal-fin rays, more anteriad placement of dorsal ocellus, dusky blind side, and cycloid scales on blind side are common to *A. antillarum* and *A. microctenus. A. antillarum* differs from *A. microctenus* in having well-developed ctenii on the scales of the ocular side (see Fig. 4), and having the 3rd, 4th, and 5th dorsal-fin rays elongated (see Fig. 3). The 5th dorsal-fin ray is reduced in length on one specimen of *A. antillarum,* similar to that of *A. microctenus.*

Well-developed ctenii on scales of ocular side of *A. antillarum* are similar to those on *A. dilecta* (see Fig. 4). This new species differs from *A. dilecta* in: usually having fewer dorsal- and anal-fin rays between origins of these fins and centers of dorsal and ventral ocelli (Table 4); lacking prominent fleshy projections on tips of some anterior dorsal-fin rays; more anteriad placement of dorsal and ventral ocelli; having the blind side dusky rather than immaculate; having cycloid scales on blind side (on a few specimens ctenoid scales on peduncle of ocular side overlap onto blind side); and having the first two dorsal-fin rays short (see Fig. 3). *A. antillarum* also differs in having the longest dorsal-fin ray longer than, or nearly equal to, head length in specimens up to about 200 mm SL, in larger specimens the longest dorsal-fin ray is shorter than head (Fig. 5); in *A. dilecta* the longest dorsal-fin ray is shorter than head on all specimens (54-213 mm SL).

A. antillarum differs more from *A. cycloidea* than from other three-spotted species of Atlantic *Ancylopsetta.* Both have cycloid scales on blind side, but ctenii on scales of ocular side are well developed on *A. antillarum* and poorly developed on *A. cycloidea* (see Fig. 4). *A. antillarum* also differs from *A. cycloidea* in having the first two anterior dorsal-fin rays reduced, and next three elongated (see Fig. 3); with increase in specimen size, the difference in length of rays becomes less pronounced (Fig. 5). Compared with *A. cycloidea, A. antillarum* has fewer dorsal-fin rays anterior to center of dorsal ocellus and a dusky blind side, and lacks prominent fleshy tips on anterior dorsal-fin rays.

A. antillarum is easily distinguished from the other three species of *Ancylopsetta* and from *Gastropsetta.* It differs from *A. dendritica* (Fig. 7C), the Pacific species, in having elongate anterior dorsal-fin rays, narrow inter-orbital width (less than ⅓ eye diameter), and in presence of cycloid scales on blind side. It differs from *A. quadrocellata* and *A. kumperae* (Figs. 8A and B), by having only three large ocellated spots on ocular side (lacking a fourth spot above the arch of lateral line), cycloid scales on blind side, naked maxillary and interorbital space, and elongate anterior dorsal-fin rays (none elongate in *A. kumperae,* and only slightly elongate in *A. quadrocellata*). It differs from *Gastropsetta frontalis* (Fig. 8C) in having ctenoid scales on ocular side, origin of dorsal fin behind posterior nostril of blind side, anterior profile of head with concavity anterior to upper eye, and most posterior spot over lateral line on posterior ⅓ of body; and in shape of urohyal.

Range.—*A. antillarum* is known from the Atlantic and the Antilles, off the Bahamas, Puerto Rico, the Virgin Islands, and from the Caribbean Sea off British Honduras (Fig. 6). It is found at greater depths (120-250 fathoms) than any other *Ancylopsetta.*

Name.—The name *antillarum* refers to the Antilles (genitive plural), where this species was first collected.

Holotype.—USNM 255358-F2, SILVER BAY 3512, 23°05′N, 78°49′W, 225-250 fms, 7 Nov 1961, 296 mm SL, female.

Paratypes.—ANSP 102912: SILVER BAY 2472, 24°40′N, 79°16′W, 200 fms, 7 Nov 1960, 2 specimens (203-238 mm SL). BLBG: SILVER BAY

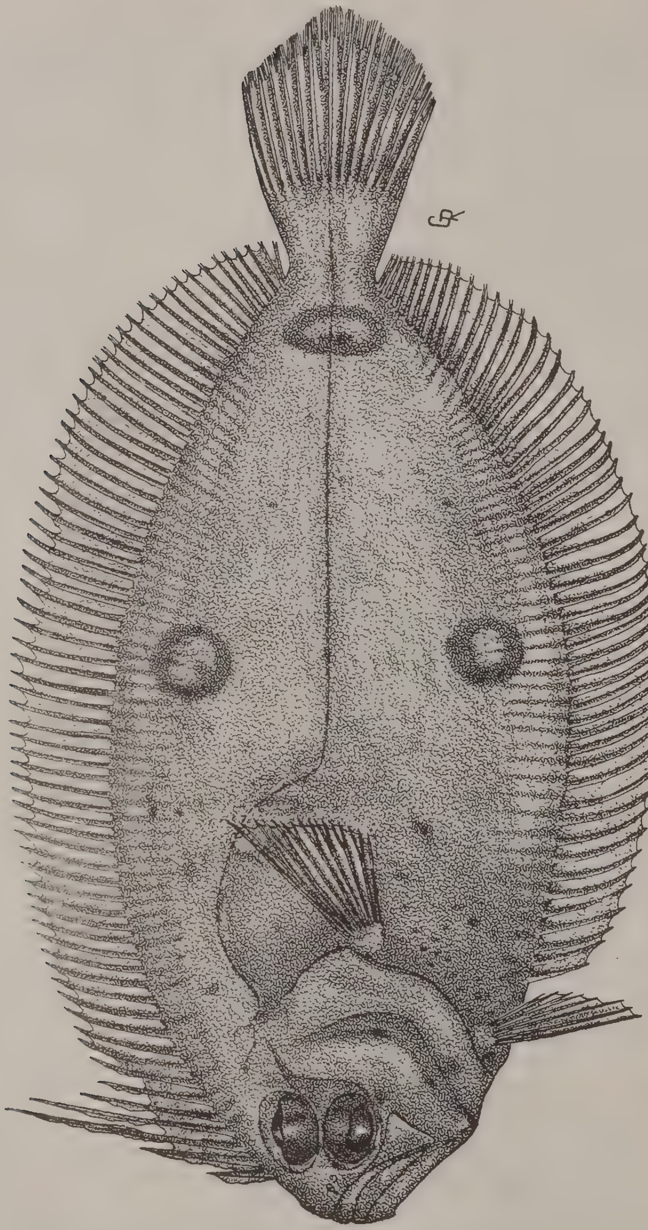

FIGURE 2. Holotype *Ancylopsetta microctenus.*

2468, 23°52′N, 79°11′W, 210-200 fms, 6 Nov 1960, 1 (136). BMNH 1965.6.17.4: SILVER BAY 2468, 1 (135); 1965.6.17.3: SILVER BAY 2477, 1 (235). CNHM 66760: SILVER BAY 2457, 23°34′N, 79°07′W, 250 fms, 5 Nov 1960, 1 (282); 65496: OREGON 2645, 18°13′N, 67°20′W, 210 fms, 5 Oct 1959, 1 (163). MCZ 44132: SILVER BAY 2471, 1 (231). SU 62529: SILVER BAY 2477, 1 (230). TABL: SILVER BAY 2468, 23°52′N, 79°11′W, 210-200 fms, 6 Nov 1960, 2 (152-232); SILVER BAY 2470, 24°25′N, 79°13′W, 125 fms, 7 Nov 1960, 1 (49); SILVER BAY 2471, 24°34′N, 79°16′W, 150 fms, 7 Nov 1960, 2 (81-111); SILVER BAY 2472, 1 (255); SILVER BAY 2477, 25°13′N, 79°13′W, 200 fms, 8 Nov 1960, 1 (290); OREGON 3636, 17°17′N, 87°59′W, 125 fms, 10 June 1962, 1 (195). UMML 17384: SILVER BAY 2472, 1 (265); 7601: OREGON 2643, 18°03′N, 64°27′W, 150-180 fms, 5 Oct 1959, 1 (216). USNM 255358-F6: SILVER BAY 2468, 1 (98); 255358-F5: SILVER BAY 2471 1, (74); 255358-F4: SILVER BAY 3471, 27°23′N, 78°26′W, 212-225 fms, 25 Oct 1961, 1 (178); 255358-F3: SILVER BAY 3512; captured with the holotype, 3 (146-230); 255358-F7: OREGON 3637, 17°13′N, 87°55′W, 120-170 fms, 10 June 1962, 2 (114-132).

Ancylopsetta microctenus, new species

Fig. 2; Tables 2, 3, and 4

Diagnosis.—An *Ancylopsetta* with three ocellated spots on ocular side. Scales of ocular side with poorly developed ctenii not projecting beyond scale margin. First and 2nd dorsal-fin rays short, 3rd and 4th rays long, 5th shorter but slightly longer than succeeding rays. Dorsal-fin rays anterior to a vertical through center of dorsal ocellus 32-36. Blind side dusky, becoming less noticeable on larger specimens.

Description.—Counts and measurements of selected characters of the holotype and 21 paratypes are shown in Table 2, and other counts and measurements in Tables 3 and 4. Additional measurements discussed in the text were taken on all specimens but are not shown in Tables 2, 3, or 4. Range of characters in the text is followed by the value for the holotype in parentheses.

Head length 27-32 (27) per cent SL. Diameter of upper eye 7-9 (7) per cent SL and 25-29 (26) per cent HL, about equal to lower eye (eyes distended and distorted on some specimens brought up from great depths). Snout length 19-22 (20) per cent HL. Snout to preopercle distance 77-82 (80) per cent HL. Upper jaw length 43-47 (47) per cent HL. Lower jaw length 52-57 (55) per cent HL. Body depth 44-50 (47) per cent SL.

Dorsal-fin rays total 64-71 (69), anterior to a vertical through center of dorsal ocellus 32-36 (36), posterior to the vertical 29-37 (33). Longest dorsal-fin ray 13-37 (25) per cent SL, longer than head to 130 mm SL,

TABLE 2

Ancylopsetta microctenus—Selected Measurements (in Per Cent of Standard Length and Head Length) and Counts for the Holotype* and Paratypes

	Standard length in mm	92	116	124	128	133	147	153	155	156	163	163	164	166	171	173	174	175	185	187	194*	202	205
Per cent SL	Head length	31	31	32	30	32	30	30	30	30	30	30	32	30	30	29	30	28	29	29	27	31	30
	Longest dorsal-fin ray	36	37	33	34	27	25	24	30	19	31	30	26	21	24	31	34	15	29	27	25	13	14
	Length pelvic fin ocular side	22	19	18	19	16	15	17	17	14	18	21	18	18	17	20	20	13	16	14	16	15	18
	Body depth	48	46	44	45	46	47	46	47	50	45	48	47	44	47	46	47	48	47	49	47	46	48
	Head length in mm	29	36	39	38	42	44	45	46	46	48	48	52	50	51	50	52	49	54	55	53	62	61
Per cent HL	Length first dorsal-fin ray	29	28	28	22	21	27	30	32	26	28	26	27	25	25	26	26	25	25	24	26	22	22
	Length second dorsal-fin ray	48	39	40	52	48	38	40	45	40	40	56	42	31	45	43	48	40	44	47	42	32	39
	Length third dorsal-fin ray	116	118	105	114	84	83	79	102	65	105	91	83	71	[1]	100	106	[1]	99	91	91	43	44
	Length fourth dorsal-fin ray	103	101	101	91	82	70	76	94	59	86	100	69	70	81	106	115	53	92	76	76	42	46
	Length fifth dorsal-fin ray	52	49	41	52	48	43	43	50	39	49	57	42	38	46	48	52	48	58	41	52	35	48
Counts	DFR ant. cent. of D. Oc.[2]	35	36	34	35	35	35	33	35	35	34	34	34	35	35	35	35	32	35	35	36	35	34
	DFR pos. cent. of D. Oc.[3]	32	29	31	30	31	33	32	32	31	33	33	31	35	33	33	35	32	34	34	33	32	37
	AFR ant. cent. of V. Oc.[4]	20	21	21	20	22	21	21	23	22	22	23	22	22	23	22	22	20	22	22	22	21	22
	AFR pos. cent. of V. Oc.[5]	30	31	29	32	30	31	31	31	30	32	32	30	32	31	32	32	31	33	34	32	31	33
	Dorsal-fin rays	67	65	65	65	66	68	65	67	66	67	67	65	70	68	68	70	64	69	69	69	67	71
	Anal-fin rays	50	51	50	52	52	52	52	54	52	54	55	52	54	54	54	55	51	55	56	54	52	55
	Scales on lateral line	71	69	68	75	70	67	71	72	73	70	75	69	73	64	68	73	68	71	73	72	71	70

[1] = Broken.
[2] = DFR ant. cent. of D. Oc. = Number of dorsal-fin rays anterior to a vertical midline of the dorsal ocellus.
[3] = DFR pos. cent. of D. Oc. = Number of dorsal-fin rays posterior to a vertical midline of the dorsal ocellus.
[4] = AFR ant. cent. of V. Oc. = Number of anal-fin rays anterior to a vertical midline of the ventral ocellus
[5] = AFR pos. cent. of V. Oc. = Number of anal-fin rays posterior to a vertical midline of the ventral ocellus.

TABLE 3

VERTEBRAL COUNTS FOR SPECIES OF *Ancylopsetta* AND *Gastropsetta*

Species	Abdominal		Caudal					Total					
	10	11	24	25	26	27	28	34	35	36	37	38	39
A. antillarum	27	–	–	2	24	1	–	–	2	24	1	–	–
A. cycloidea[1]	31	–	9	22	–	–	–	9	22	–	–	–	–
A. dilecta[1]	56	–	–	1	21	34	–	–	1	21	34	–	–
A. microctenus	19	1	2	18	–	–	–	1	19	–	–	–	–
A. dendritica[1]	–	7	–	–	–	–	7	–	–	–	–	–	7
A. kumperae[1]	15	–	–	1	11	3	–	–	1	11	3	–	–
A. quadrocellata[1]	19	49	–	5	60	3	–	–	1	21	44	2	–
G. frontalis[1]	27	–	–	2	5	16	4	–	2	5	16	4	–

[1] In part from Tyler, 1959.

either longer or shorter than head between 130 and 180 mm SL, and shorter than head above 180 mm SL. First ray length 21-32 (26) per cent HL, 2nd ray 31-56 (42) per cent HL, 3rd ray 43-118 (91) per cent HL, 4th ray 42-115 (76) per cent HL, 5th ray 35-58 (52) per cent HL.

Anal-fin rays total 50-56 (54), anterior to a vertical through center of ventral ocellus 20-23 (22), posterior to vertical 29-34 (32).

Pectoral-fin rays ocular and blind sides 10-11 (10), on ocular side two most dorsal rays and most ventral ray unbranched, others branched. Pectoral-fin length ocular side 17-20 (17) per cent SL; length blind side 12-18 (14) per cent SL.

Pelvic-fin ray 6 (6). Pelvic-fin length ocular side 13-22 (16) per cent SL, longest pelvic rays much shorter than head, not more than twice pelvic-fin length of blind side. Pelvic-fin length blind side 10-14 (12).

Caudal-fin rays 17 (17); two outermost principal rays on dorsal and ventral edge unbranched, others branched.

Gillrakers, including rudiments, total 9-11 (10), lower limb 7-8 (7), upper limb 2-3 (3).

Vertebrae 10 + 24-25 and 11 + 24 (11-24).

Characters of the nostrils essentially similar to those described for *A. antillarum.*

Scales in lateral line, total 64-75 (72), curved portion 25-30 (27), straight portion 37-49 (45). Scales of ocular side with weak, poorly developed ctenii not extending beyond posterior margin of scales (superficially resembling cycloid scales, Fig. 4). Scales on blind side cycloid, deeply imbedded. Naked and scaled areas of blind and ocular sides essentially the same as in *A. antillarum.*

Teeth uniserial, about equally developed both sides. Teeth on dentary fewer and larger than teeth of upper jaw, except for anterior canines which are of about equal length in both jaws. Teeth of upper jaw essentially as

TABLE 4

FREQUENCY DISTRIBUTIONS OF NUMBERS OF DORSAL- AND ANAL-FIN RAYS ANTERIOR TO A VERTICAL THROUGH MIDLINE OF DORSAL AND VENTRAL OCELLI, FOR FOUR ATLANTIC SPECIES OF *Ancylopsetta* WITH THREE SPOTS

	Dorsal-fin rays																	
Species	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46
A. dilecta	–	–	–	–	–	–	–	–	–	2	1	6	5	10	3	9	5	1
A. cycloidea	–	–	–	–	–	–	–	5	14	8	4	2	–	–	–	–	–	–
A. microctenus	–	–	–	1	1	6	13	2	–	–	–	–	–	–	–	–	–	–
A. antillarum	2	3	9	7	6	1	–	–	–	–	–	–	–	–	–	–	–	–

	Anal-fin rays											
Species	18	19	20	21	22	23	24	25	26	27	28	29
A. dilecta	–	–	–	–	1	–	6	13	12	7	3	–
A. cycloidea	–	–	–	4	4	9	14	2	–	–	–	–
A. microctenus	–	–	4	5	11	3	–	–	–	–	–	–
A. antillarum	2	13	8	3	2	–	–	–	–	–	–	–

in *A. antillarum*. Vomer, palatines, and tongue toothless. Pharyngeal teeth in three rows.

Three prominent ocellated spots on ocular side. Posterior spot ovate, located on lateral line just anterior to peduncle. Anterior two spots located just in advance of midpoint of body, one below the dorsal fin, other above anal fin (Fig. 2). Pigmentation in center of and around ocellated spots variable, but with the following basic pattern: pale center (with or without dark spot or spots) surrounded by dark area, darker area encompassed by diffuse light brown area.

General body color on ocular side pale brown to tan (preserved material). Fin rays and inter-radial membranes on ocular side partially covered with melanophores, except inter-radial membranes of pectoral fin. Pigmentation of ocular side generally not extending onto blind side. Caudal more profusely pigmented than other fins.

Blind side straw-colored and partially overlaid with melanophores, resulting in dusky appearance. Pigmentation of pectoral and pelvic fins on blind side similar to that of body, with few or no melanistic spots. Membrane overlying rays of anal, dorsal, and caudal fins dark, but inter-radial membranes of these fins usually clear. The head and first few dorsal fin rays with little if any duskiness.

Variable dark red or orangish bands on both sides of body overlying musculature of rays of dorsal and anal fins, sometimes also present on cheeks and above opercle (bands composed of masses of oil globules; differences in density of accumulated oil globules account for variation in color).

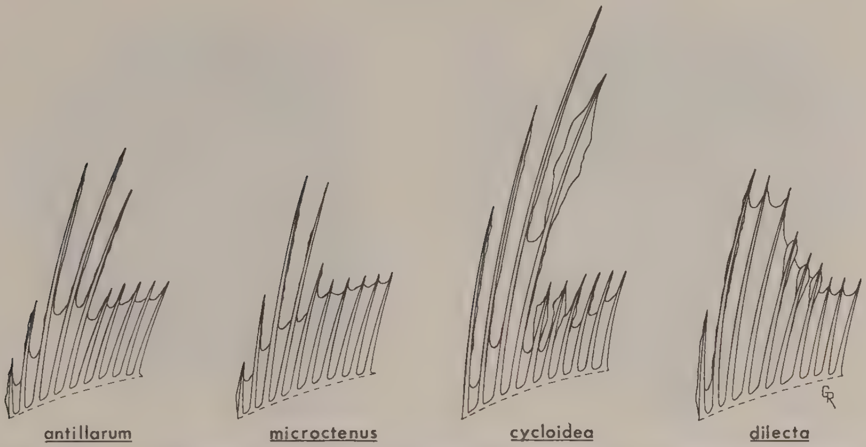

FIGURE 3. Configuration of first 10 dorsal-fin rays of the three-spotted species of Atlantic *Ancylopsetta.*

Relationships.—*A. microctenus* is most closely related to *A. antillarum,* and next to *A. cycloidea.* Similarities and differences between *A. microctenus* and *A. antillarum* have been discussed under Relationships, for *A. antillarum.*

Poorly developed ctenii on scales of ocular side (see Fig. 4) and cycloid scales covering entire blind side of *A. microctenus* are features similar to those of *A. cycloidea. A. microctenus* and *A. cycloidea* also may have elongate anterior dorsal-fin rays that can be longer or shorter than head (see text of *A. cycloidea*). *A. microctenus* differs from *A. cycloidea* in: having the first two dorsal-fin rays short and the next two long, rather than a short first ray followed by three long rays (see Fig. 3); having a dusky rather than an immaculate blind side; and lacking prominent fleshy tips on some anterior dorsal-fin rays.

Of the three-spotted Atlantic species of *Ancylopsetta, A. microctenus* differs most from *A. dilecta.* Compared with *A. dilecta, A. microctenus* has poorly developed ctenii on scales of ocular side (see Fig. 4), first two dorsal-fin rays short (see Fig. 3) and usually fewer rays in the dorsal and anal fins between origins of these fins and centers of dorsal and ventral ocelli (Table 4), dusky blind side, and no prominent fleshy tips on anterior dorsal-fin rays.

A. microctenus differs from *A. dendritica, A. kumperae, A. quadrocellata, and G. frontalis* in the same characters as does *A. antillarum* (discussed under Relationships in species account of *A. antillarum*).

Range.—*A. microctenus* is known only from the Caribbean Sea off Honduras and Nicaragua from depths of 100-160 fathoms (Fig. 6).

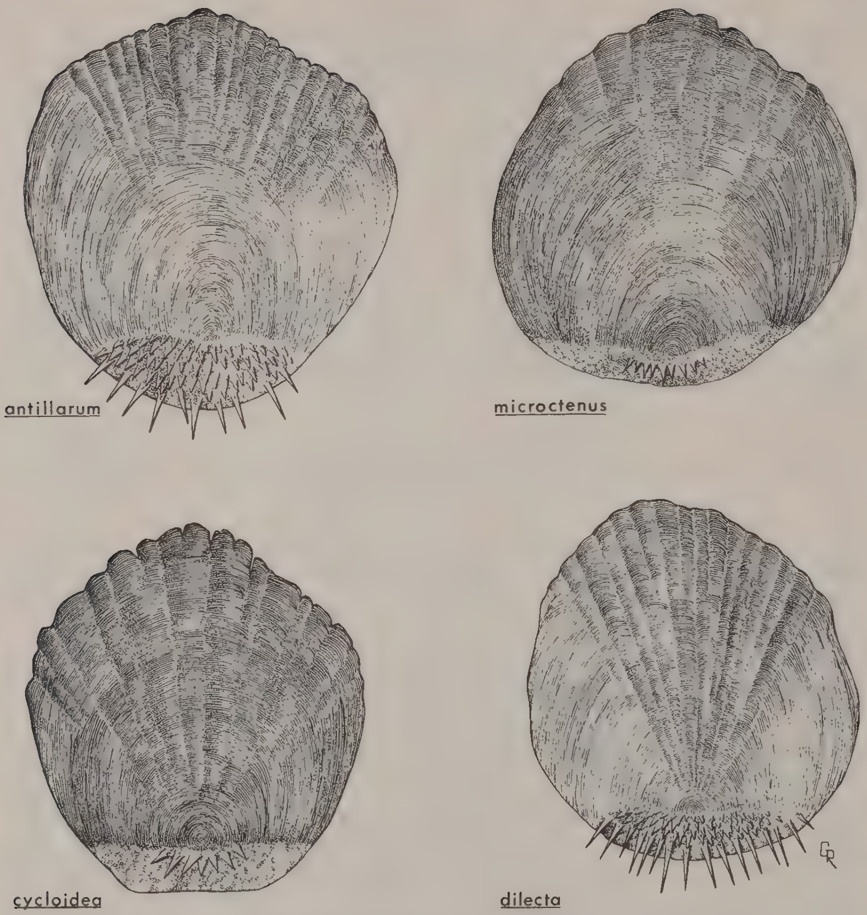

FIGURE 4. Scales from ocular side of adults of three-spotted species of Atlantic *Ancylopsetta,* illustrating development of ctenii; removed from an area just above the lateral line at about the posterior ⅔ of SL. *A. antillarum* USNM 255358-F3 (220 mm SL); *A. microctenus* ANSP 102913 (166 mm SL); *A. cycloidea* paratype USNM 159794 (97 mm SL); *A. dilecta* TABL (154 mm SL).

Name.—The name *microctenus* (*micro,* small; *ktenos,* comb) refers to the microscopic ctenii on scales of ocular side. This name is a noun in apposition.

Holotype.—USNM 255358-F1: Oregon 3625, 16°26′N, 81°35′W, 120 fms, 6 June 1962, 194 mm SL, female.

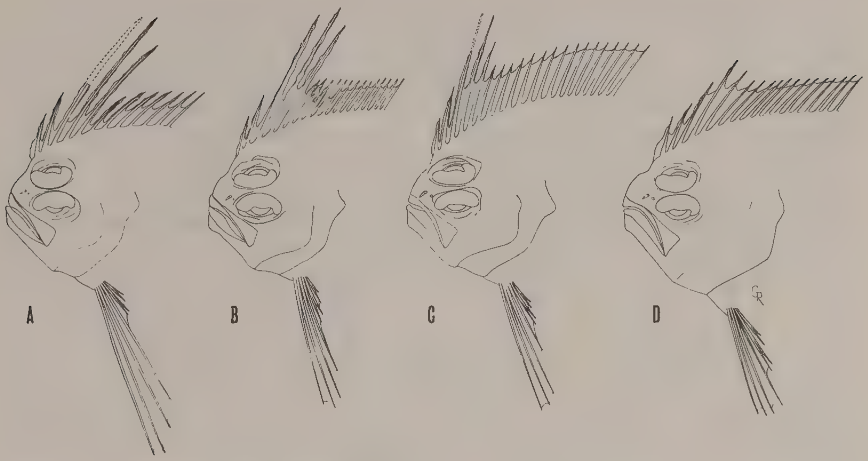

FIGURE 5. Head series of *Ancylopsetta antillarum,* illustrating ontogenetic growth of elongate anterior dorsal-fin rays and pelvic-fin rays of the ocular side with increasing size of fish. Specimens from left to right: 82, 152, 198, and 265 mm SL.

Paratypes.—ANSP 102913: OREGON 3622, 16°01′N, 81°08′W, 145-150 fms, 6 June 1962, 2 specimens (164-166 mm SL). BMNH 1965.6.17.6: OREGON 3566, 1 (202); 1965.6.17.5: OREGON 3626, 1 (155). CNHM 65489: OREGON 1894, 15°15′N, 81°19′W, 145 fms, 25 Aug 1957, 2 (128-153). MCZ 44133: OREGON 3626, 1 (163). SU 62533: OREGON 3622, 1 (174): TABL: OREGON 3566, 14°10′N, 81°58′W, 150-160 fms, 21 May 1962, 1 (124); OREGON 3622, 2 (93-133); OREGON 3626, 16°45′N, 81°27′W, 150 fms, 7 June 1962, 1 (205). UMML 17381: OREGON 3566, 1 (175); 17383: OREGON 3626, 1 (171). USNM 255358-F10: OREGON 3566, 2 (116-147); 255358-F8: OREGON 3578, 12°28′N, 82°25′W, 100 fms, 23 May 1962, 1 (156); 255358-F9: OREGON 3626, 4 (163-187).

Ancylopsetta cycloidea Tyler
Fig. 7A

Ancylopsetta cycloidea Tyler, 1959:140, Fig. 1 (type description and illustration, OREGON station 2021, 07°18′N, 53°32′W, 100 fathoms).

Diagnosis.—An *Ancylopsetta* with three ocellated spots on ocular side. Scales of ocular side with poorly developed ctenii which do not project beyond scale margin. First dorsal-fin ray shorter than following three, 3rd (occasionally 4th) longest, 5th ray very short, about equal in length to succeeding rays. Dorsal-fin rays anterior to a vertical through center of dorsal ocellus 36-40. Blind side immaculate.

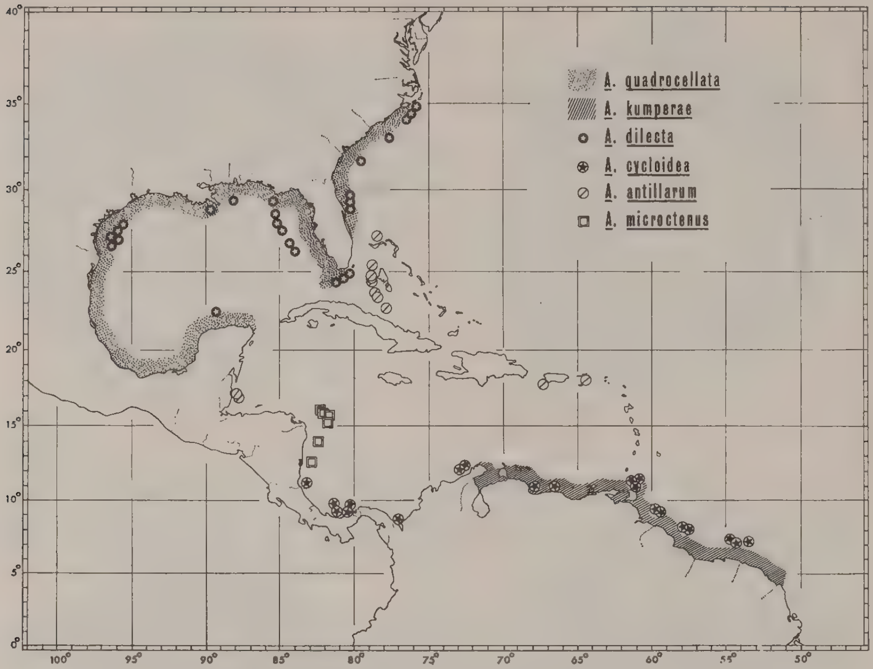

FIGURE 6. Distribution of Atlantic species of *Ancylopsetta.*

Description.—Measurements as percentage of standard length: body depth 44-52; head length 28-32; longest dorsal-fin ray length 20-52; pelvic-fin length ocular side 16-63 (Atlantic specimens 30-63, Caribbean specimens 16-23), blind side 11-15; pectoral-fin length ocular side 18-22, blind side 15-20.

Measurements as percentage of head length: diameter of upper eye 26-32, about equal to lower eye; snout length 16-21; snout to preopercle distance 74-81; upper-jaw length 40-49; lower-jaw length 52-57.

Dorsal-fin rays 62-68; anal-fin rays 48-52; pectoral-fin rays ocular side 10-11, blind side 9-11; gillrakers, including rudiments, total 8-11, lower limb 6-7, upper limb 1-4; scales in lateral line 67-76; vertebrae 10 + 24-25 (Table 3). Selected counts and measurements recorded from 50 specimens. Supplemental data extracted from Tyler's (1959) paper: lower limit, pectoral-fin length ocular side; lower and upper limit, lower-jaw length; upper limit, snout length, snout to preopercle distance, and number of scales in lateral line.

Ocular side brownish or tan (preserved material), three large ocellated spots, arrangement similar to that of *A. antillarum* and *A. microctenus* (Fig. 7A); blind side immaculate.

Scalation.—Ctenoid scales on the ocular side, about one to eight microscopic ctenii on each scale (see Fig. 4). "In ctenoid . . . the teeth are typically part of the posterior field" (Lagler, Bardach, & Miller, 1962: 117, Fig. 4.4:116); and "Ctenii are tooth-like structures found in the posterior field of the ctenoid scale. . . . Ctenii may appear in a single row parallel to the margin or in two or more rows; they may be prominent or weak. . . ." (Van Oosten, 1957:238). The poorly developed ctenii can be seen only under magnification and are easily discernible after alizarin staining. Ctenii on the scales adjacent to the lateral line are most prominent, and become increasingly difficult to discern near dorsal and anal fins and in abdominal region.

Dorsal Fin.—Tyler (1959:140) stated that in *A. cycloidea* the length of the elongated anterior dorsal-fin rays is greater than the length of the head, but in no other *Ancylopsetta* are these rays as long as the head. In recently acquired large specimens of *A. cycloidea* from the Caribbean these elongate fin rays are shorter than the head and in some specimens of both *A. antillarum* and *A. microctenus* they are longer than the head. No other known species of *Ancylopsetta* has the same configuration of first five dorsal-fin rays as *A. cycloidea* (see Figs. 3, 7, and 8). Thirty-two of 50 specimens examined were collected in the Atlantic from Tobago to French Guiana, and the remaining 18 in the Caribbean from Venezuela to Nicaragua. In all Atlantic specimens (70-159 mm SL) the longest dorsal-fin ray is longer than the head. In specimens from the Caribbean (105-228 mm SL) dorsal-fin ray length is longer or shorter than the head. In one Caribbean specimen the anterior elongate fin rays are broken; in the remaining 17 specimens the longest dorsal-fin ray is longer than the head in specimens up to 131 mm SL, either longer or shorter than the head between 131 and 161 mm SL, and shorter than the head in fish larger than 161 mm SL. The ontogenetic growth (positive to negative allometry) of elongate anterior dorsal-fin rays in *A. antillarum, A. microctenus,* and Caribbean *A. cycloidea* suggests that we could expect these rays of Atlantic *A. cycloidea* to be shorter than the head in larger specimens.

Pelvic Fin.—The Atlantic population of *A. cycloidea* can readily be separated from the Caribbean population by relative length of pelvic fin on ocular side. In 31 specimens from the Atlantic (70-159 mm SL), length of pelvic fin is greater than head length (in another specimen the pelvic fin rays are broken), but in 18 specimens (105-228 mm SL) from the Caribbean it is much shorter than the head, as in *A. microctenus.* This difference may represent a genotypic separation between the two populations, but more specimens must be examined to confirm this, particularly from Venezuela, Trinidad, and Tobago.

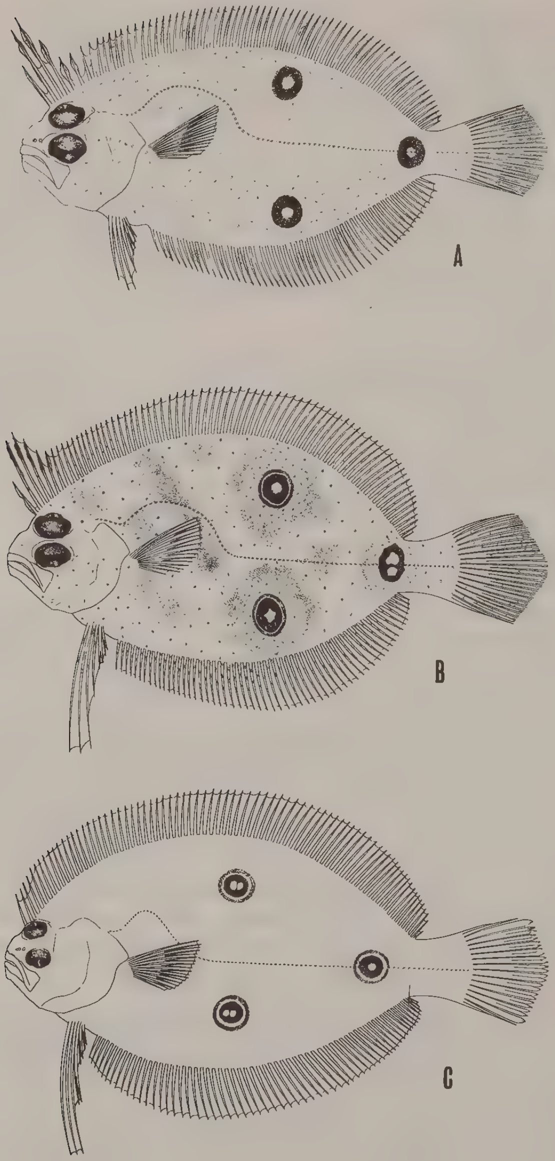

FIGURE 7. A—*A. cycloidea* (see text for comments on variation in lengths of anterior dorsal-fin rays and pelvic-fin rays of ocular side between Atlantic and Caribbean forms); B—*A. dilecta;* C—*A. dendritica.*

Relationships.—*A. cycloidea* is most closely related to *A. dilecta,* and next to *A. microctenus.* Similarities and differentiating characteristics among *A. cycloidea, A. dilecta,* and *A. microctenus* are discussed under species accounts of *A. dilecta* and *A. microctenus.*

Range.—The previously reported range for *A. cycloidea* was French Guiana to British Guiana in 80 to 115 fathoms (Tyler, 1959:147). Known distribution is extended from French Guiana to southern Nicaragua in depths of 36 to 140 fathoms (Fig. 6).

Specimens Examined.—ANSP 102911: OREGON 4446, 10°54′N, 68°01′W, 100 fms, 10 Oct 1963, 1 specimen (169 mm SL). BMNH 1965.6.17.2: OREGON 4920, 12°13′N, 72°34′W, 100 fms, 1 June 1964, 1 (134); 1965.6.17.1: OREGON 5031, 11°12′N, 60°53.5′W, 40-42 fms, 22 Sept 1964, 1 (133). CNHM 65490: OREGON 1904, 11°34′N, 83°07′W, 125 fms, 10 Sept 1957, 1 (156); 64455: Paratype, OREGON 1987, 09°36′N, 59°44′W, 80 fms, 4 Nov 1957, 1 (89); 64456: Paratypes, OREGON 2021, 07°18′N, 53°32′W, 100 fms, 8 Nov 1957, 8 (83-151); 65491: OREGON 2221, 09°22′N, 59°43′W, 50 fms, 28 Aug 1958, 3 (71-127); 65492: OREGON 2231, 08°32′N, 58°42′W, 45-48 fms, 29 Aug 1958, 3 (70-81); 65493: OREGON 2232, 08°31′N, 58°37′W, 48-46 fms, 29 Aug 1958, 7 (76-131); 65494: OREGON 2286, 07°26′N, 54°49′W, 105-120 fms, 8 Sept 1958, 5 (113-159); 65495: OREGON 2290, 07°27′N, 54°32′W, 110 fms, 8-9 Sept 1958, 1 (133); 66761: OREGON 4465, 1 (150). MCZ 44134: OREGON 4465, 1 (193). SU 62540: OREGON 4446, 1 (134). TABL: OREGON 3587, 09°18′N, 80°25′W, 75 fms, 29 May 1962, 1 (119); OREGON 3595, 09°02′N, 81°26′W, 100 fms, 30 May 1962, 1 (160); OREGON 4465, 10°45′N, 66°37′W, 125 fms, 17 Oct 1963, 1 (228); OREGON 4898, 08°53.8′N, 76°51.6′W, 100 fms, 27 May 1964, 4 (107-152); OREGON 4913, 12°09′N, 72°47′W, 100 fms, 1 June 1964, 1 (178); OREGON 5024, 11°08′N, 60°56′W, 36-45 fms, 21 Sept 1964, 1 (155). UMML 17382: OREGON 4446, 1 (152). USNM 159794: Paratype, OREGON 2021, 1 (97); 255358-F14: OREGON 3585, 09°12′N, 81°30′W, 135-140 fms, 25 May 1962, 1 (191); 255358-F11: OREGON 3590, 09°18′N, 80°22′W, 125 fms, 29 May 1962, 1 (184); 255358-F13: OREGON 4920, 12°13′N, 72°34′W, 100 fms, 1 June 1964, 1 (161); 255358-F12: OREGON 5025, 11°08′N, 60°58′W, 40-48 fms, 21 Sept 1964, 1 (137).

Ancylopsetta dilecta (Goode & Bean)

Fig. 7B

Notosema dilecta Goode & Bean, 1883:193 (type description, locality 32°31′50″N, 78°45′W, 75 fathoms, 4 specimens).—Goode & Bean, 1896:437 (description, distribution, and illustration).

Notosema dilectum, Jordan & Evermann, 1898:2635 (description and type locality).

Paralichthys stigmatias, Goode, 1884:182 (casual mention of locality, South Carolina).

Ancylopsetta dilecta, Jordan, 1887:134 (description and distribution).—Jordan & Goss, 1889:250 (distribution).—Norman, 1934:126 (description, distribution, and deposition of type).

Diagnosis.—An *Ancylopsetta* with three ocellated spots on ocular side. Ctenoid scales on both ocular and blind side, but not covering entire blind side. Elongate anterior dorsal-fin rays never longer than head. Dorsal-fin rays anterior to a vertical through center of dorsal ocellus 38-46. Blind side immaculate.

Description.—Measurements as percentages of standard length: body depth 45-53; head length 25-31; longest dorsal-fin ray length 14-25; pelvic-fin length ocular side 21-35, blind side 7-16; pectoral-fin length ocular side 16-23, blind side 12-18.

Measurements as percentages of head length: diameter of upper eye 24-32, about equal to lower eye; snout length 17-22; snout to preopercle distance 77-86; lower-jaw length 51-60.

Dorsal-fin rays 68-79; anal-fin rays 53-60; pectoral-fin rays ocular side 10-12, blind side 10-11; gillrakers, including rudiments, total 7-11, lower limb 6-9, upper limb 1-3; scales in lateral line 73-82; vertebrae 10 + 25-27 (Table 3).

Ocular side brownish (preserved material), three large ocellated spots essentially the same shape and arrangement as in *A. cycloidea* (Fig. 7B).

Relationships.—This species is most closely related to *A. cycloidea,* and next to *A. antillarum.* Fleshy projections on some anterior dorsal-fin rays, shortened first dorsal-fin ray followed by several elongated rays (see Fig. 3), and absence of melanophores on blind side are common to *A. dilecta* and *A. cycloidea. A. dilecta* differs from *A. cycloidea* in having well-developed ctenii on the scales of the ocular side (see Fig. 4) and ctenoid scales partially covering blind side, and in configuration of first five dorsal-fin rays (see Fig. 3). Similarities and differences between *A. dilecta* and *A. antillarum* have been discussed under Relationships of *A. antillarum.*

Range.—Range previously reported for *A. dilecta* was North Carolina to Texas in 40-112 fathoms (Tyler, 1959:147). Specimens I examined extend the geographic range to Yucatan in Mexico, and the bathymetric range to 32-200 fathoms (Fig. 6).

Specimens Examined.—BLBG: OREGON 2922, 27°54′N, 95°45′W, 32 fms, 18 Aug 1960, 1 specimen (70 mm SL). CNHM 46330: OREGON 273, 29°09′N, 85°59′W, 110 fms, 18 Feb 1951, 1 (197); 64011: OREGON 602, 29°31.5′N, 86°21.4′W, 80 fms, 12 July 1952, 1 (153); 61307:

Oregon 945, 29°48′N, 86°37′W, 67 fms, 21 Mar 1954, 1 (204); 61308: Oregon 957, 27°03′N, 84°16′W, 75 fms, 3 Apr 1954, 1 (152); 65497: Combat 384, 34°54′N, 75°25′W, 75 fms, 17 June 1957, 1 (114); 45421: 28°50′N, 85°43′W, 88 fms, 4 (185-213); 45084: 27°29′N, 96°16′W, 58 fms, 1 (163); 45086: 27°20′N, 96°20′W, 200 fms, 7 (165-184). TABL: Silver Bay 289, 27°47′N, 95°42′W, 40-45 fms, 4 Feb 1958, 3 (163-184); Silver Bay 301, 29°18′N, 88°02′W, 60-65 fms, 13 Mar 1958, 1 (187); Silver Bay 460, 29°38′N, 80°14′W, 75 fms, 13 June 1958, 1 (154); Silver Bay 480, 30°00′N, 80°12′W, 180 fms, 19 June 1958, 1 (154); Silver Bay 1670, 33°11′N, 77°18′W, 105-100 fms, 27 Feb 1960, 1 (100); Silver Bay 2381, 24°41′N, 80°48′W, 47-50 fms, 26 Oct 1960, 1 (68); Silver Bay 2384, 24°44′N, 80°40′W, 60 fms, 26 Oct 1960, 4 (73-120); Silver Bay 2390, 24°42′N, 80°44′W, 50 fms, 26 Oct 1960, 4 (75-89); Silver Bay 2732, 28°41′N, 80°01′W, 80 fms, 2 Feb 1961, 1 (169); Silver Bay 2930, 34°45′N, 75°32′W, 75 fms, 13 Mar 1961, 4 (86-117); Silver Bay 2932, 34°35′N, 75°40′W, 90 fms, 13 Mar 1961, 1 (110); Silver Bay 5397, 32°01′N, 79°10′W, 75-80 fms, 7 Dec 1963, 1 (152); Oregon 4083, 27°56′N, 84°46′W, 100 fms, 4 Dec 1962, 2 (175-189). TU 2741: Oregon 219, 23°00′N, 89°36′W, 76 fms, 10 Jan 1951, 4 (175-186); 13011: 28°41.5′N, 89°32′W, 30 Aug 1955, 1 (162).

Ancylopsetta dendritica Gilbert
Fig. 7C

Ancylopsetta dendritica Gilbert, 1890:121 (type description, locality Albatross 3022, 30°58′30″N, 113°17′15″W, 11 fathoms).—Gilbert & Starks, 1904:199 (description, genus *Ramularia* not recognized).—Norman, 1934:125 (description, distribution, and deposition of type).

Ramularia dendritica Jordan & Evermann, 1898:2633 (description, described the genus *Ramularia*, type *Ancylopsetta dendritica*).

Hippoglossina sabanansis Boulenger, 1899:4 (type description, locality Rio Sabana, Darien, Panama).

Pseudorhombus dendritica, Meek & Hildebrand, 1928:972 (description and distribution).

Diagnosis.—An *Ancylopsetta* with three ocellated spots on ocular side. Ctenoid scales covering entire body, including wide interorbital area, which is at least ⅓ diameter of eye. Anterior dorsal-fin rays not elongate.

Description.—Measurements as approximate percentages of standard length: body depth 50-54; head length 26-28; pelvic-fin length ocular side 28-35, blind side 12-15; pectoral-fin length ocular side 18-20, blind side 15-16.

Measurements as approximate percentages of head length: diameter of upper eye 18-20, about equal to lower eye; snout length 15-17; snout to preopercle distance 65-66; upper-jaw length 37-40, shorter than lower jaw 45-48.

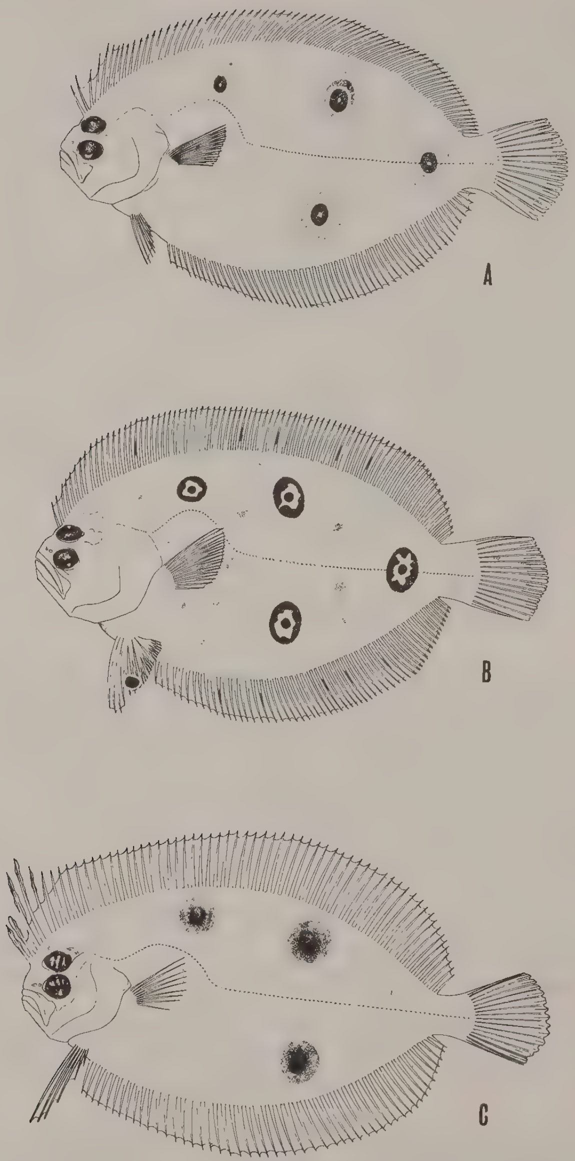

FIGURE 8. A—*A. quadrocellata;* B—*A. kumperae;* C—*G. frontalis.*

Dorsal-fin rays 76-84; anal-fin rays 63-67 (John E. Fitch, personal communication, said he had one specimen 308 mm SL from the Gulf of California with an anal ray count of 59); pectoral-fin rays on both ocular and blind sides 11-12; gillrakers, including rudiments, total 7-9, lower limb 5-7, upper limb 2; scales in lateral line 86-90; vertebrae 11 + 28 (Table 3). Selected counts and measurements recorded from only 2 specimens. Supplemental data for some upper and lower limits of counts and measurements extracted from Norman (1934) and Tyler (1959).

Ocular side brownish (preserved material), position and shape of ocellated spots on ocular side essentially the same as in Atlantic species of three-spotted *Ancylopsetta* (Fig. 7C).

Relationships.—The only species of *Ancylopsetta* known to occur in the Pacific, *A. dendritica,* has certain morphological similarities to both three-spotted and four-spotted species of Atlantic *Ancylopsetta.* It and the two four-spotted Atlantic species have ctenoid scales covering entire body, including the interorbital space; and either no elongation of the anterior dorsal-fin rays (*A. dendritica* and *A. kumperae*) or only slight elongation of these rays (*A. quadrocellata*). *A. dendritica* can readily be distinguished from the two four-spotted species by its considerably longer ocular pelvic fin and absence of ocellated spot over arch of lateral line. Similarities among *A. dendritica* and the Atlantic three-spotted species are: extensive elongation of ocular pelvic fin (excluding *A. microctenus,* Caribbean specimens of *A. cycloidea,* and large specimens of *A. antillarum*) and presence of only three ocellated spots on the ocular side. It can be readily distinguished from the three-spotted species by its short anterior dorsal-fin rays, ctenoid scales covering entire blind side, and greater interorbital width.

Range.—Range of *A. dendritica* was recorded from Gulf of California to Panama by Tyler (1959:147), and extended to Ecuador by Orces (1959:88). The only recorded depth of capture is 11 fathoms. John E. Fitch (personal communication) said that at one time fair numbers were being shipped to the San Diego fresh fish markets from shrimp-trawling operations in the northern Gulf of California; one specimen was taken by trawl in 23-27 fms.

Specimens Examined.—USNM 81035: Panama mkt., 10 Feb 1912, 2 specimens (154-181 mm SL).

Ancylopsetta quadrocellata Gill
Fig. 8A

Ancylopsetta quadrocellata Gill, 1864:224 (type description, locality Pensacola, Florida).—Jordan & Goss, 1889:250 (distribution).—Jordan & Evermann, 1898:2634 (description and distribution).—Norman, 1934:127 (description, distribution, and deposition of type).

Pseudorhombus quadrocellatus Jordan & Gilbert, 1879:370 (description).
Paralichthys ommatus Jordan & Gilbert, 1882:824 (type description).—Jordan & Gilbert, 1883:616 (description).—Jordan & Swain, 1884:234 (locality, Cedar Keys, Florida).

Diagnosis.—An *Ancylopsetta* with four ocellated spots on ocular side, generally with light-colored or pale centers (these may be absent on some large specimens). Anteromost dorsal-fin rays slightly elongate. Ctenoid scales covering entire body. Interorbital area and distal portion of maxillary scaled.

Description.—Measurements as percentages of standard length: body depth 53-63; head length 25-32; pelvic-fin length ocular side 12-22, blind side 10-15; pectoral-fin length ocular side 16-18, blind side 12-16.

Measurements as percentages of head length: diameter of upper eye 18-24, about equal to lower eye; snout length 18-20; snout-to-preopercle distance 69-73; upper-jaw length 37-46, shorter than lower 46-54.

Dorsal-fin rays 67-76; anal-fin rays 54-61; pectoral-fin rays ocular side 10-12, blind side 10-11; gillrakers, including rudiments, total 8-10, lower limb 6-7, upper limb 2-3; scales in lateral line 80-90.

Ocular side brownish (preserved material), four ocellated spots, smallest over curved portion of lateral line, shape and position of the other three similar to those in the three-spotted *Ancylopsetta* (Fig. 8A).

Vertebrae.—This species has 10 or 11 abdominal vertebrae. The count of 9 recorded by Jordan & Evermann (1898:2635), suggests they failed to count the small vertebra attached to the skull. Tyler (1959:146) listed only 10 abdominal vertebrae for this species, he later (personal communication) informed me that his data were in part incorrect; corrected vertebral counts for specimens of *A. quadrocellata* he X-rayed are: 1 (10-25), 10 (10-26), 1 (11-25), and 4 (11-26). I have examined these and 52 others, or a total of 49 from North Carolina to central Florida in the Atlantic and 19 from southern Florida to southern Texas in the Gulf of Mexico. All Atlantic specimens have 11 abdominal vertebrae, and all from the Gulf of Mexico have 10. This probably represents a genotypic separation between the two populations. The species distribution may be disjunct rather than continuous; I have no records of it between Dry Tortugas and Jupiter, Florida.

Relationships.—*A. quadrocellata* is most closely related to *A. kumperae*. Of the seven species of *Ancylopsetta*, only these two possess the following combination of characteristics: ctenoid scales over entire body, four ocellated spots in similar position on ocular side, and short pelvic fin on ocular side. *A. quadrocellata* differs from *A. kumperae* in having some anterior dorsal-fin rays slightly elongate and the centers of ocelli generally pale, and in lacking an ocellated spot on pelvic fin of ocular side and extensive branching of inner rays of pelvic fin of ocular side.

Range.—*A. quadrocellata* is known from Cape Hatteras, North Carolina, to Jupiter, Florida, at Tortugas, and from Cape Sable, Florida, along the Gulf coast of the United States to Corpus Christi, Texas, in depths of 2 to 80 fathoms. Tyler (1959:147) reported on its occurrence off Campeche, Mexico.

Specimens Examined.—BLBG: SILVER BAY 3773, 26°19′N, 82°03′W, 6 fms, 19 Mar 1962, 2 specimens (60-80 mm SL). TABL: SILVER BAY 656, 30°12′N, 86°38′W, 15 fms, 3 July 1958, 1 (200); SILVER BAY 1273, 34°46′N, 76°04′W, 17 fms, 12 Sept 1959, 1 (219); SILVER BAY 1353, 33°03′N, 78°58′W, 7-8 fms, 19 Oct 1959, 1 (195); SILVER BAY 1390, 32°24′N, 79°28′W, 15-16 fms, 26 Oct 1959, 1 (148); SILVER BAY 1523, 31°13′N, 80°10′W, 22 fms, 14 Jan 1960, 1 (154); SILVER BAY 1553, 29°39′N, 81°06′W, 10-9 fms, 19 Jan 1960, 1 (186); SILVER BAY 1663, 34°20′N, 77°22′W, 9-8 fms, 26 Feb 1960, 1 (40); SILVER BAY 4246, 27°58′N, 80°04′W, 21 fms, 28 Aug 1962, 1 (177); SILVER BAY 5399, 31°53′N, 79°34′W, 31 fms, 8 Dec 1963, 2 (181-193); Commercial Trawling Area, Brunswick, Georgia, 1 (132). UMML 536: 24°45′ to 24°50′N, 82°10′ to 82°30′W, 5 Oct 1955, 1 (177); 721: 24°45′ to 24°50′N, 82°10′ to 82°30′W, 19 Dec 1955, 1 (179); 3689: 25°04′30″N, 81°04′30″W, 14 Aug 1958, 1 (129).

Ancylopsetta kumperae Tyler
Fig. 8B

Ancylopsetta kumperae Tyler, 1959:143, fig. 2 (type description and illustration, COQUETTE station 297, 06°45′N, 55°17′W, 24 fathoms).

Diagnosis.—An *Ancylopsetta* with four ocellated spots on ocular side, centers of which are dark. A 5th ocellated spot is over the distal portion of the 3rd and 4th pelvic-fin rays of ocular side. Anterior dorsal-fin rays not elongated. Extensive branching of pelvic-fin rays on ocular side, particularly of last two fin rays, these normally splitting into more than four terminal elements. Interorbital area and broadened posterior part of maxillary scaled.

Description.—Measurements as percentages of standard length: body depth 49-55; head length 24-30; pelvic-fin length ocular side 15-18, blind side 10-15; pectoral-fin length ocular side 14-19, blind side 12-16.

Measurements as percentages of head length: diameter of upper eye 19-26, about equal to lower eye; snout length 16-20; snout to preopercle distance 71-75; lower-jaw length 50-58.

Dorsal-fin rays 72-84; anal-fin rays 57-63; pectoral-fin rays ocular side 11-13, blind side 11-12; gillrakers, including rudiments, total 8-9, lower limb 6-7, upper limb 2; scales in lateral line 78-99; vertebrae 10 + 25-27 (Table 3). These counts and measurements were recorded from 8 specimens, and from data presented by Tyler (1959).

Ocular side brownish (preserved material), centers of ocelli dark, ocellated spot on pelvic fin of ocular side; position of four ocelli on ocular side essentially the same as in *A. quadrocellata* (Fig. 8B).

Relationships.—This species is most closely related to *A. quadrocellata.* Similarities and differences have been discussed under Relationships of *A. quadrocellata.*

Range.—Previously reported from the northernmost coast of Brazil to Surinam in 23 to 50 fathoms (Tyler, 1959:147); subsequent capture of *A. kumperae* from the Caribbean extends the distribution north to at least eastern Colombia (Fig. 6).

Specimens Examined.—TABL: OREGON 4180, 06°44′N, 54°29′W, 30 fms, 20 Feb 1963, 2 specimens (179-200 mm SL); OREGON 4393, 12°32′N, 71°04′W, 46 fms, 25 Sept 1963, 1 (168); OREGON 4402, 12°19′N, 70°34′W, 40 fms, 27 Sept 1963, 3 (125-164); OREGON 4471, 10°16′N, 65°30′W, 32 fms, 19 Oct 1963, 1 (116); OREGON 4481, 11°14′N, 64°13′W, 30 fms, 22 Oct 1963, 1 (110).

Gastropsetta Bean

Gastropsetta Bean, 1895:633 (Type species *Gastropsetta frontalis* Bean, 1895, by monotypy).

Sinistral, body ovate and compressed, greatest depth about ½ SL. Anterior profile of head evenly convex. Eyes separated by naked narrow ridge. Jaws and dentition about equally developed both sides; teeth uniserial both jaws, conical, small, increasing in size anteriorly; lower jaw included. Gillrakers very short and broad. Tip of first interhaemal spine not projecting through skin in advance of anal fin. Lateral line well developed on both sides of body. Origin of dorsal well in advance of anterior edge of upper eye, commencing above anterior nostril on blind side. Pectoral and pelvic fins of ocular side longer than on blind side, pelvic fin of ocular side elongate. Scales small, well embedded, cycloid, covering entire body. Vent on blind side, above origin of first anal-fin ray; posterior edge of pelvic fin on blind side attached to membrane adjacent to vent. Urogenital pore on ocular side, opposite vent. Urohyal lacking a well-developed keel on its anteroventrally-directed arm; keel no wider than diameter of shaft from which it projects. Monotypic.

Gastropsetta frontalis Bean
Fig. 8C

Gastropsetta frontalis Bean, 1895:633-634 (type description and illustration, locality ALBATROSS 2317, 24°25′45″N, 81°46′45″W, 45 fathoms).—Jordan & Evermann, 1898:2636 (description and locality of type specimens).—Norman, 1934:128 (description, distribution, and deposition of type).

Diagnosis.—A species with three ocellated spots on ocular side; two above lateral line—anterior one above arch of lateral line and posterior one slightly behind vertical midline; ventral spot below posterior dorsal spot. No spot on lateral line. Scales small, cycloid, over entire body. Origin of dorsal fin well in advance of anterior edge of upper eye, commencing above anterior nostril of blind side. Anterior profile of head convex (see Fig. 8C).

Description.—Measurements as percentages of standard length: body depth 45-55; head length 23-30; longest dorsal-fin ray length 13-38; pelvic-fin length ocular side 15-78, blind side 8-12; pectoral fin of ocular side longer than that of blind side.

Measurements as percentages of head length: diameter of upper eye 25-31, about equal to lower eye; snout length 18-23; snout to preopercle distance 68-75; upper-jaw length 35-43, shorter than lower-jaw length 43-51.

Dorsal-fin rays 58-65; anal-fin rays 46-53; pectoral-fin rays ocular side 10-11, blind side 9-11; gillrakers, including rudiments, total 9-14, lower limb 6-8, upper limb 3-6; scales in lateral line 95-112; vertebrae 10 + 25-28 (Table 3).

Ocular side light tan to dark brown (preserved material); three large ocellated spots, not arranged as in *Ancylopsetta* (Fig. 8C).

Dorsal Fin.—Literature references imply that length of longest dorsal-fin ray is nearly equal to or greater than head length. On four of 16 specimens examined these fin rays are longer than the head (101-167 mm SL, 111-138 per cent HL), on six they are slightly shorter than the head (139-225 mm SL, 76-96 per cent HL), and on six they are considerably shorter than the head (199-252 mm SL, 49-64 per cent HL). The relative growth of the dorsal-fin rays in this species is similar to that of *A. microctenus,* i.e., the longest dorsal-fin ray is longer than head on smaller specimens, but becomes proportionally shorter with increasing body size and is shorter than head on large specimens.

Pelvic Fin.—Pelvic fin of ocular side is longer than on blind side at all sizes. In the two smallest specimens I examined (101-117 mm SL), the longest pelvic-fin ray of ocular side is at least four times as long as on blind side; in the remaining 14 specimens (139-252 mm SL) the ratio of length of longest pelvic-fin ray, ocular to blind side, is about 2:1 or less.

Relationships.—Of species in the genus *Ancylopsetta, G. frontalis* is probably most closely related to *A. cycloidea.* The elongated anterior dorsal-fin rays and the fleshy projections on some of these rays are common to both species. The differences are discussed under the section Generic Relationships.

Range.—Previously reported from North Carolina to Yucatan, Mexico (Tyler, 1959:147); specimens I examined extend the range into the Bahamas (Great Inagua) and south to Panama, in depths from 19 to 100 fathoms.

Specimens Examined.—BLBG: SILVER BAY 2398, 24°38′N, 80°58′W, 35 fms, 27 Oct 1960, 1 specimen (183 mm SL). TABL: SILVER BAY 1342, 33°05′N, 77°47′W, 51-50 fms, 18 Oct 1959, 1 (117); SILVER BAY 2361, 24°58′N, 80°22′W, 26-30 fms, 25 Oct 1960, 1 (175); SILVER BAY 2409, 24°35′N, 81°07′W, 32-30 fms, 28 Oct 1960, 1 (101); SILVER BAY 3502, 20°54′N, 73°37′W, 100-75 fms, 5 Nov 1961, 1 (252); SILVER BAY 3758, 29°52′N, 80°32′W, 19-21 fms, 24 Feb 1962, 1 (235); SILVER BAY 5387, 31°31′N, 79°46′W, 28 fms, 5 Dec 1963, 1 (145); SILVER BAY 5395, 32°00′N, 79°28′W, 32-35 fms, 6 Dec 1963, 1 (159); SILVER BAY 5406, 31°50′N, 79°33′W, 35 fms, 12 Dec 1963, 1 (167); SILVER BAY 5677, 34°37′N, 75°44′W, 34-37 fms, 17 Apr 1964, 2 (199-225); OREGON 3577, 12°32′N, 82°25′W, 85 fms, 23 May 1962, 2 (139-204); OREGON 3587, 09°18′N, 80°25′W, 75 fms, 29 May 1962, 2 (199-230); OREGON 3611, 12°30′N, 82°29′W, 80 fms, 3 June 1962, 1 (240).

GENERIC RELATIONSHIPS

The three subfamilies of Bothidae, Paralichthinae, Bothinae, and Scophthalminae, are differentiated by the form and relative length of the pelvic fins, and by structure of the vertebrae. In Paralichthinae (including *Ancylopsetta* and *Gastropsetta*) the pelvic fins are short-based, do not extend forward onto the urohyal, are supported by the pelvic bone, and are inserted behind the cleithrum. Abdominal (precaudal) vertebrae have closed haemal arches; caudal vertebrae have no transverse apophyses (Norman, 1934:38).

Paralichthinae of the western North Atlantic include, in addition to *Ancylopsetta* and *Gastropsetta,* the following genera: *Paralichthys, Hippoglossina, Syacium, Citharichthys, Cyclopsetta, Etropus, Trichopsetta, Engyophrys,* and *Monolene.* The closely related *Ancylopsetta* and *Gastropsetta* can be separated from other genera of Paralichthinae in the western North Atlantic by the following combination of characters: neither pelvic fin on median line; pelvic-fin rays of ocular side elongate, distinctly longer than on blind side; anterior dorsal-fin rays elongate (excluding *A. kumperae* and *A. dendritica*); and three or four large ocellated spots on ocular side (Figs. 1, 2, 7, & 8).

Four external and a single internal character can be used to separate *Ancylopsetta* from *Gastropsetta:* presence or absence of ctenii on scales of ocular side, form of anterior profile, position of dorsal-fin origin, presence or absence of large spot on lateral line, and shape of anteroventrally directed arm of urohyal.

All species of *Ancylopsetta* have ctenoid scales on ocular side (see text for *A. cycloidea*). These species fall into two groups, one with prominent well-developed ctenii that extend beyond posterior margin of scale, and another with weak, poorly developed ctenii that do not (scales of second group superficially resemble cycloid scales). Five species of *Ancylopsetta* have well-developed ctenii on scales of ocular side; only on *A. cycloidea* and *A. microctenus* are they poorly developed. In addition to changes in degree of development of ctenii, scales vary from all ctenoid to all cycloid. In *A. dendritica, A. quadrocellata,* and *A. kumperae* the body is completely covered with scales having well-developed ctenii; the other species have both ctenoid and cycloid scales. In *A. dilecta* the ocular side is completely covered with scales having well-developed ctenii, but the blind side has both ctenoid and cycloid scales; in the majority of specimens cycloid scales outnumbered ctenoid scales on blind side. On *A. antillarum* the ocular side is covered with scales having well-developed ctenii, but the blind side has only cycloid scales (on a few specimens ctenoid scales on peduncle of ocular side overlap onto blind side). On both *A. cycloidea* and *A. microctenus* the scales on ocular side have poorly developed ctenii and those on the blind side are cycloid (scalation superficially similar to that of *G. frontalis*). I do not consider type of scalation as the best taxonomic character for separation of these genera because of variation in degree of development of ctenii, but scalation nevertheless is useful in separating them.

Location of origin of dorsal fin, in combination with the form of the anterior profile of the head, will always separate these two genera. In *Gastropsetta* the origin of dorsal fin is well in advance of upper eye, and is located above anterior nostril on blind side; and the mass of tissue in the area immediately in front of anterior edge of upper eye, associated with the dorsal fin, gives the anterior profile of head a smooth convex curve. In *Ancylopsetta* the origin of the dorsal fin is above, slightly in front of, or slightly behind anterior edge of upper eye, commencing behind posterior nostril on blind side; and the absence of a tissue mass in front of anterior edge of upper eye results in a moderate to well-defined concavity in anterior profile. In all six Atlantic species this concavity is very evident, but it is less distinct in the Pacific species, *A. dendritica*. All *Ancylopsetta* have a large spot on lateral line just in front of the caudal peduncle, but *Gastropsetta* has no spot on the lateral line nor on the posterior ⅓ of the body.

Osteological characteristics of the urohyal (as discussed by Tyler, 1959:146, fig. 3) also separate these two genera. *Ancylopsetta* has a keel on the lower anteroventrally-directed arm which is well developed and more than twice as wide as the diameter of the shaft from which it projects. The keel is narrowest in *A. dendritica,* the Pacific species, but even here it is still considerably wider than in *Gastropsetta*. In

Gastropsetta the keel on the lower arm is no wider than the diameter of the shaft from which it projects.

From this discussion I draw the following conclusions: the type of scales on the ocular side is useful in separating these two genera; the other three characteristics are taxonomically important because in none of them do species of *Ancylopsetta* overlap with *Gastropsetta.* Degree of development of the concavity anterior to the upper eye and keel on the anteroventrally-directed arm of the urohyal is not so great in *A. dendritica* as in the Atlantic *Ancylopsetta.*

KEY TO THE SPECIES OF *ANCYLOPSETTA* AND *GASTROPSETTA*

A. Origin of dorsal fin well in advance of anterior margin of upper orbit; no large spot on lateral line (3 body spots); head with smooth convex dorsal profile, no notch in front of upper eye; scales on ocular side cycloid. (Atlantic) .... *Gastropsetta frontalis* (Fig. 8C)

AA. Origin of dorsal fin above, behind, or slightly in advance of anterior margin of orbit; large spot present on lateral line on posterior ⅓ of body (3 or 4 body spots); head with concave dorsal profile, a notch in front of upper eye; scales on ocular side ctenoid (ctenii microscopic in two species, scales smooth to the touch). (Atlantic and Pacific) .... (Ancylopsetta) B

B. Four ocellated spots on ocular side, not arranged in pattern of an isosceles triangle, anterior spot above curved portion of lateral line C

BB. Three ocellated spots on ocular side, arranged in pattern of an isosceles triangle, no ocellated spot above curved portion of lateral line .... D

C. No dark ocellated spot on distal portion of pelvic fin on ocular side, some anterior dorsal-fin rays slightly elongate, longer than succeeding rays, centers of ocelli generally pale. (Atlantic) .... *A. quadrocellata* (Fig. 8A)

CC. Dark ocellated spot on distal portion of pelvic fin on ocular side, none of the anterior dorsal-fin rays longer than succeeding rays, centers of ocelli dark. (Atlantic) ...... *A. kumperae* (Fig. 8B)

D. Anterior dorsal-fin rays not elongated; well-developed ctenoid scales covering entire body; relatively wide, scaled interorbital space, at least ⅓ diameter of the eye. (Pacific) .... *A. dendritica* (Fig. 7C)

DD. Anterior dorsal-fin rays elongated; ctenoid scales not covering entire body, some or all scales on blind side cycloid; narrow, naked interorbital space, less than ⅓ diameter of eye. (Atlantic) .... E

E. Ctenii on scales of ocular side well developed, projecting beyond scale margin, rough to the touch (see Fig. 4) .... F

EE. Ctenii on scales of ocular side microscopic, not well developed, not projecting beyond scale margin, smooth to the touch (see Fig. 4) .... G

F. Rays between origin of dorsal fin and center of dorsal ocellus 29 to 34 (Table 4); first two fin rays short, next three long (may be longer or shorter than head), succeeding rays short and of about equal length; no prominent fleshy projections on tips of anterior dorsal-fin rays (see Fig. 3); blind side dusky, less noticeable on some large specimens .... *A. antillarum* (Fig. 1)

FF. Rays between origin of dorsal fin and center of dorsal ocellus 38 to 46 (Table 4); first fin ray short, second or third ray longest (never longer than head), succeeding rays gradually decreasing in length through sixth or seventh ray; prominent fleshy projections on tips of some anterior dorsal-fin rays (see Fig. 3); blind side immaculate .... *A. dilecta* (Fig. 7B)

G. First two dorsal-fin rays short, next two long; no prominent fleshy projections on tips of anterior dorsal-fin rays (see Fig. 3); blind side dusky; pelvic fin of ocular side less than twice length of pelvic fin of blind side .... *A. microctenus* (Fig. 2)

GG. First dorsal-fin ray short, next three long; prominent fleshy projections on tips of anterior dorsal-fin rays (see Fig. 3); blind side immaculate; pelvic fin of ocular side may be more or less than twice length of pelvic fin of blind side .... *A. cycloidea* (Fig. 7A)

SUMARIO

REVISIÓN DEL GÉNERO DE PECES LENGUADOS *Ancylopsetta* (HETEROSOMATA: BOTHIDAE) CON DESCRIPCIONES DE DOS NUEVAS ESPECIES DE LAS ANTILLAS Y EL MAR CARIBE

Seis especies de *Ancylopsetta* y el monotípico *Gastropsetta* se sabe que habitan el Océano Atlántico Occidental, Golfo de México y Mar Caribe en profundidades de 2 a 250 brazas. Una especie, *A. dendritica,* se encuentra en el Océano Pacífico Oriental y el Golfo de California. Seis de las ocho especies en estos dos géneros tienen tres manchas en forma de ojos en el lado ocular; *A. quadrocellata* y *A. kumperae* tienen cuatro.

Se dan descripciones e ilustraciones para dos nuevas especies, *A. antillarum* y *A. microctenus.* Se discuten sus relaciones con otros miembros de este género y el monotípico *Gastropsetta.* Además se dan un diagnóstico, una descripción breve, ilustración, distribución y una lista de ejemplares examinados para cada especie de *Ancylopsetta* y *Gastropsetta.* Se da una clave para la identificación de especies de estos dos géneros.

Varios caracteres pueden ser usados para separar el género *Ancylopsetta*

de *Gastropsetta:* presencia o ausencia de escamas ctenoideas en el lado ocular, posición del origen de la aleta dorsal, forma del perfil anterior de la cabeza, forma del anteroventralmente dirigido brazo de urohyal y presencia o ausencia de una gran mancha en la línea lateral.

Las nuevas especies, *A. antillarum* y *A. microctenus,* pueden ser distinguidas de la otra *Ancylopsetta* del Atlántico que tiene tres manchas, por los caracteres siguientes: el lado ciego es oscuro en lugar de inmaculado; los dos primeros rayos de la aleta dorsal son cortos, en lugar del primero sólamente; falta de proyecciones carnosas en los extremos de los rayos anteriores de la aleta dorsal; y localización de las dos manchas anteriores inmediatamente delante de la línea media vertical del cuerpo. Las nuevas especies son fácilmente separables una de la otra por el grado de desarrollo de los ctenii en las escamas del lado ocular; los ctenii están bien desarrollados en estas escamas en *A. antillarum,* pero pobremente desarrollados (las escamas superficialmente parecen ser cicloides) en *A. microctenus.* También, la longitud del quinto rayo de la aleta dorsal difiere: en *A. antillarum* es largo, pero en *A. microctenus* es corto, sólo ligeramente más largo que los rayos siguientes.

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SODIUM, POTASSIUM, AND CHLORIDE TRANSPORT AND MEMBRANE POTENTIALS IN VALONIA VENTRICOSA

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In 1891 Meyer discovered that coenocytic cells of the marine alga *Valonia* have a high potassium and low sodium content. *Valonia* and other giant-celled algae subsequently became popular organisms for studies of ion permeability and transport, mainly because large quantities of vacuolar sap could be collected without contamination by protoplasm or extracellular fluid. From these early studies came Osterhout's theories on the nature of protoplasmic surfaces and his models of membrane transport by carrier molecules (Osterhout, 1931, 1940).

Electrical studies on *Valonia,* which were conducted with the permeability and transport studies, were initiated by Osterhout *et al.* (1924, 1927) and pursued later by Blinks (1940, 1955). *Valonia* was, in fact, the first cell in which a steady electric potential between internal and external solutions, *i.e.,* sap and sea water, was demonstrated. Osterhout's discovery that the vacuole of *Valonia* is electrically positive to external sea water did not seem unusual, since few data from other cells were available for comparison. The positive vacuole potential appears now, however, to be restricted to *Valonia* and its close relatives (see Blinks, 1949).

Later work on ion transport in *Valonia* suggested a relation between net K^+ uptake and external phosphate concentration (Mullins, 1949) and the existence of separate mechanisms for Na^+ and K^+ transport (Scott and Hayward, 1955). Another marine coenocyte, *Halicystis ovalis,* was shown to extrude Na^+ at the plasmalemma and actively absorb Cl^- at the tonoplast (Blount and Levedahl, 1960). Similar transports of Na^+ and Cl^- were found in *Nitellopsis,* a brackish-water characean (MacRobbie and Dainty, 1958a). Additional work on marine algae is summarized by Gutknecht (1965a).

In *Valonia* the relations between ion concentrations and fluxes and the electric potentials have not been studied. Therefore it is not known with certainty which ions are actively transported nor at which membrane, plasmalemma or tonoplast, the transport takes place. My objective is to answer these questions by using electrochemical methods similar to those of Dainty, MacRobbie and others working on the fresh-water Characeae (see reviews by Dainty, 1962, 1964).

I will show that the ionic and electrical properties of *Valonia ventricosa* differ in several respects from those of other plant cells. The high salt content of the vacuole is produced by an inward transport of Na^+ and especially K^+ at the tonoplast, whereas Cl^- uptake into the vacuole appears to be a passive process. The electric potential of the cytoplasm is highly negative to the vacuole, which contrasts with the small or zero potential across the tonoplast of other cells. Like most other plant and animal cells, *Valonia* actively extrudes Na^+ at the plasmalemma, and its cytoplasm is electrically negative to the external sea water.

METHODS

Culture methods

The *Valonia* cells used in this study were either 1–3 cm. diameter, shipped by air from Puerto Rico, or 0.3–0.8 cm. diameter, grown from aplanospores in the laboratory. Similar results were obtained with both sizes. The experimental and culture medium was an enriched sea water similar to that described by Keck (1964). Briefly, the medium consisted of natural sea water plus nitrate, phosphate, soil extract, and enough artificial sea salts (Utility Chemical Co., Paterson, N. J.) to raise the salinity to about 37‰—similar to the water from which the cells were collected.

Cultures were started with young cells, called aplanospores, which formed spontaneously from the protoplasm of mature coenocytes (see Steward, 1939). Soon after spore formation, the outer wall of the coenocyte was cleaned with alcohol to remove epiphytes. The wall was then pierced with a syringe, and a suspension of spores was withdrawn and transferred to the sea-water medium. Cultures started in this way were free from contaminating algae, which was important since other species usually grow faster than *Valonia.*

The cells were grown in large fingerbowls, and the medium was changed at about two-week intervals. The temperature was 25 ± 1° C., and illumination was 3000–4000 lux, 8–12 hr./day (natural daylight plus fluorescent lighting). Some of the bowls contained marble chips, as prescribed by Steward (1939); within several weeks many cells became attached to the marble substrate by rhizoid processes. This attachment did not appear necessary for normal growth and development, however, for in three months both attached and unattached cells grew to a diameter of about 0.5 cm. and showed similar ionic and electrical properties.

Chemical measurements

Sap from large cells was obtained by piercing the cell surface with a syringe and withdrawing about 200 μl. Sap from small cells was collected by washing the cell for one minute in 0.9 M sucrose, blotting with absorbent tissue, puncturing with a sharp needle, and gently squeezing. The sap was uncontaminated by protoplasm, as indicated by the absence of chloroplasts in the sample.

Protoplasm was collected by cutting a large coenocyte in half and allowing the sap to drain out. The wall and adhering protoplasm were washed gently for 20–25 seconds in a large volume of Tris-sulfate buffer, pH 7.7–7.8, approximately isosmotic to sap (1.14 molal). The protoplasm, along with some buffer, was gently scraped from the wall with a scalpel, taken up in a capillary tube, and centrifuged in a hematocrit centrifuge for 10 minutes at about 12,000 g. The protoplasm fraction was forced out of the tube and weighed. The protoplasm from several large cells was pooled to give 20–40 mg. wet weight per sample. The protoplasm was combined with the supernatant buffer, diluted to 5 ml. with 0.1 N HNO_3, and allowed to extract for several days.

The amount of water in the protoplasm was measured in separate samples by drying overnight at 100–110° C. Na^+, K^+, and Cl^- were measured with a Beckman DU flame spectrophotometer and an Aminco-Cotlove chloride titrator. The osmotic pressure of sea water, sap, and Tris was measured with a Fiske osmometer.

This method of collecting protoplasm was not quantitative, for there was always some loss during washing and scraping. The amounts agreed approximately, however, with those predicted from Doyle's (1940) measurements of protoplasm volume and density. No attempt was made to separate the cytoplasm from the chloroplasts, which comprise 60–70% of the protoplasm volume in *V. ventricosa* (Doyle, 1935, 1940).

Electrical measurements

Electric potentials of the vacuole and cytoplasm were measured with microcapillary electrodes and a high-impedance voltmeter (Keithley Model 600A). The electrical circuit was similar to that described by Gutknecht (1965a). Micropipets were drawn from 1-mm. Pyrex tubing and filled with 0.6 *M* KCl by boiling under reduced pressure. Tip diameters ranged from <1 μ to about 10 μ. The larger tips were necessary to pierce the tough outer wall of old cells. Electrode tip potentials in either sea water or artificial sap were <2 mv.

To measure the vacuole potential, a microelectrode was forced through the cell wall and underlying protoplasm (5–10 μ thick) until the tip protruded about 1 mm. into the vacuole. The puncture was made with the aid of a micromanipulator and dissecting microscope. The potential difference between vacuole and sea water was initially low, then rose gradually to a maximum and remained steady (±2 mv) for many hours. The cells were illuminated during both the electrical and flux measurements (3000–4000 lux), which was important because the vacuole potential in *V. ventricosa* is sensitive to light (Marsh, 1939).

The electric potential of the cytoplasm was measured in aplanospores 5–15 hours old and 100–300 μ in diameter. These young cells were largely protoplasm rather than vacuole, and their thin wall offered little resistance to microelectrode penetration. The cells were held by gentle suction, similar to the method of Eckert (1965). When the electrode tip entered the cytoplasm, the potential rose rapidly to a maximum, then usually decreased slowly after 1–2 minutes. This decrease was due possibly to a cytoplasmic sealing process like that in *Nitella* (Walker, 1955). Potentials that were steady (±2 mv) for 1–2 minutes were recorded.

Aplanospores of fairly uniform age were obtained by cutting a large cell in half and holding it in sea water for several hours. During this time the protoplasm changed from a continuous layer into a large number of multinucleate spores, 20–300 μ in diameter (see Doyle, 1940). Alternatively, a small coenocyte was centrifuged at 1000 *g* for 10 minutes and the protoplasm, concentrated at one end of the cell, was allowed to stand for several hours in sea water. Spores formed by the latter method were usually larger but gave similar results.

Flux measurements

Ion fluxes between vacuole and sea water were measured in spherical cells of *Valonia,* 5–6 mm. in diameter and 60–110 mg. in weight. The small rhizoidal cells and hapteron cells on the surface of the main vesicle were removed with forceps. Unidirectional fluxes were measured with radioisotopes, Na^{22}, K^{42}, and Cl^{36}. Conventional detectors were used (Baird-Atomic Model 510 and Nuclear Chicago Model C-115). Tracer specific activities were high enough that the concentrations of stable ions in the radioactive media were increased less than 1%. Net fluxes were measured by the weight increase of a cell during an influx experiment (1–3 days). This was possible because the intracellular ion concentrations were constant and the average rate of growth was about 1 mg./day. Efflux was calculated from the unidirectional influx minus the net influx. Efflux of Na^+ and K^+ was also measured directly from the rate of isotope efflux into a large non-labeled environment. Both methods gave similar results, but the former method was preferred because it provided simultaneous estimates of both influx and efflux in a single cell.

To measure the influx from sea water to vacuole, a weighed cell was placed in 10 ml. of labeled medium under constant illumination. Cells were removed after 20–50 hours, washed for one minute in non-active medium, blotted, weighed, measured, and pierced with a sharp needle. The sap was squeezed out, taken up in a calibrated pipet, and transferred to a planchet for counting. The initial influx was calculated by the equation

$$M_i = \frac{C_i^* C_o V}{t C_o^* A}$$

where M_i is the influx in M/cm^2. sec., C_i^* is the concentration of labeled ions in the sap after time t, C_o is the external ion concentration, C_o^* is the external concentration of labeled ions, V is the volume, and A is the surface area of the spherical cells. The specific activity of the sap at the end of the influx period was less than 10% of the specific activity outside; therefore the efflux of labeled ions during the influx measurement was neglected.

The net flux was calculated by the equation

$$M_{net} = \frac{\Delta W C_i}{A t}$$

where M_{net} is the net influx in M/cm^2. sec., ΔW is the weight increase during time t, and C_i is the internal ion concentration.

Efflux was estimated either by subtracting the net flux from the unidirectional influx, or from direct measurements of the rate of isotope efflux into a large non-labeled environment by the equation

$$M_o = \frac{2.3 C_i V}{t A} \log \frac{C_{i0,}^*}{C_i^*}$$

where M_o is the efflux in M/cm^2. sec., and $C_{i,o}^*$ is the initial concentration of labeled ions inside.

These equations were derived from standard flux equations which treat the cells as a single compartment (see, for example, Sheppard, 1962). This was justified because the cells used for flux measurements were >99% vacuole.

RESULTS

Ion concentrations in sea water, protoplasm, and sap

Concentrations of Na^+, K^+, and Cl^- in sea water, protoplasm, and vacuolar sap are shown in Table I. Sap was analyzed from large Puerto Rican cells and from smaller cells grown in the laboratory. Protoplasm was collected only from the large coenocytes, since the small cells contained only about 0.5 μl. protoplasm per cell. Protoplasmic ion concentrations are expressed in terms of protoplasm water, which was 58.6 ± 1.0% (10) of the wet weight. Results are presented in the sequence: mean, standard error, and (in parentheses) number of measurements.

Potassium was highly concentrated in the protoplasm (434 m*M*) and especially in the vacuole (625 m*M*). Sodium was largely excluded from both protoplasm (40 m*M*) and sap (44 m*M*). The Cl^- concentration was relatively low in the protoplasm (138 m*M*), but was higher in the sap (643 m*M*) than in the external sea water. These concentrations for the sap of *V. ventricosa* are slightly higher than those of Cooper and Blinks (1928) and are similar to those of Steward and Martin (1937).

Table I

*Concentrations of Na^+, K^+, and Cl^- in sea water and protoplasm and sap of Valonia ventricosa**

Ion	Sea water (m*M*/liter)	Protoplasm (m*M*/liter water)	Sap (m*M*/liter)
Na^+	508 ± 5 (13)	40 ± 2 (8)	44 ± 1 (18)
K^+	12.1 ± 0.2 (10)	434 ± 9 (8)	625 ± 5 (18)
Cl^-	596 ± 2 (9)	138 ± 4 (8)	643 ± 2 (10)

* Mean, SE, and number of measurements.

Electric potentials across plasmalemma and tonoplast

The potential difference between cytoplasm and sea water was −71 ± 1 mv (20). The measurements were made on cells 5–10 hours old, which were mainly protoplasm surrounded by a thin cell wall. Vacuoles in cells of this age were small and not clearly defined (see Doyle, 1935). When the electrode was forced toward the center of these cells, the potential sometimes reversed sharply from negative to positive (+6 to +14 mv), which suggested entry into a vacuole. Cells 20–30 hours old resembled mature *Valonia* in having a large vacuole surrounded by a thin layer of protoplasm. In cells of this age I was sometimes able to measure a cytoplasmic potential of −70 ± 5 mv (6), whereas the vacuole potential was +12 ± 1 mv (12).

The potential difference between vacuole and sea water in older cells (3–4 months) was +17 ± 1 mv (16), vacuole positive. These cells were illuminated continuously for 2–3 days prior to the potential measurements to simulate conditions under which ion fluxes were measured. This value agrees with the early work of Blinks (1929), who used much larger, and presumably much older, cells of *V. ventricosa*.

The vacuole potential is the algebraic sum of the potentials across plasmalemma and tonoplast. Thus, subtracting the plasmalemma potential in young cells (−71 mv) from the vacuole potential in mature cells (+17 mv) gives a tonoplast potential of about −88 mv, cytoplasm negative to vacuole. This value should be confirmed by direct measurements on large cells. I have not accomplished this, however, mainly because the cell wall is as thick as the underlying protoplasm (5–12 μ; Doyle, 1940) and cannot be penetrated easily by a glass capillary of 1 μ diameter.

These results support qualitatively the early work of Umrath (1938), who found that the potential difference between cytoplasm and sea water in *V. macrophysa* was about −20 mv. Umrath measured cytoplasmic potentials in slowly deplasmolyzing cells by allowing the protoplasm to be pierced by a stationary microelectrode inside the cell wall. His microelectrodes were filled with a too dilute solution of KCl (0.1 *M*), however, for which he was criticized by Briggs, Hope and Robertson (1961, p. 109). So, although his method was not entirely satisfactory, he concluded correctly that the cytoplasm of *Valonia* is more negative toward the vacuole than toward the external sea water.

Ion fluxes

Ion fluxes between sea water and vacuole of *V. ventricosa* are shown in Table II. Unidirectional fluxes ($\mu\mu M/\text{cm}^2$. sec.) were 3.3–3.6 for Na^+, 86–89 for K^+, and 11–18 for Cl^-. Influxes were somewhat larger than effluxes, because the cells were growing at a rate of 0.5–1.5%/day and the intracellular concentrations were constant. The net fluxes, estimated from the increase in weight and average concentration of ions in the sap, were about 0.3 for Na^+, 5.6 for K^+, and 7.6 for Cl^-.

TABLE II

Fluxes of Na^+, K^+, and Cl^- between sea water and vacuole *, **

Ion	Influx	Efflux	Net flux
Na^+	3.64 ± 0.32 (20)	3.32 ± 0.33 (20)	0.32 ± 0.03 (35)
K^+	88.7 ± 3.0 (18)	86.2 ± 3.0 (18)	5.6 ± 0.6 (33)
Cl^-	18.5 ± 1.4 (30)	10.9 ± 1.1 (30)	7.6 ± 0.5 (30)

* Mean, SE, and number of measurements.

** Units are $\mu\mu M/\text{cm}^2$. sec.

The efflux of Na^+ and K^+ from *V. ventricosa* was also measured directly from the rates of Na^{22} and K^{42} efflux into a large non-labeled environment. The cells were labeled for only a short time (1–5 hours), so that the specific activity of the protoplasm would be higher than that of the sap at the start of the efflux measurement. Some typical results are shown in Figure 1. A rapid loss of both Na^{22} and K^{42} from the wall and extracellular space was complete in about 0.5 minute. The remaining Na^{22} exchanged at a nearly uniform rate and probably represents exchange of vacuolar Na^+. The rate of K^{42} exchange was non-uniform during the first hour but was constant thereafter, presumably representing exchange of vacuolar K^+. Effluxes of Na^+ and K^+ from vacuole to sea water were estimated from the slopes of the linear parts of the curves, K^{42} B and Na^{22}, as described under Methods. The efflux of Na^+, measured between 0.3 and 65 hours, was 3.8 ± 0.3 (8) $\mu\mu M/\text{cm}^2$. sec. The efflux of K^+, measured between 1 and 26 hours, was 89 ± 9 (5) $\mu\mu M/\text{cm}^2$. sec. These values agree with those obtained by the more convenient method of subtracting the net influx from the unidirectional influx (Table II).

Preliminary calculations suggest that the exchange of intracellular K^{42} proceeds at two exponential rates. The rapidly exchanging fraction (K^{42} A) was obtained by subtracting the extrapolated portion of the slow fraction (K^{42} B) from the total activity. The faster rate probably represents exchange of protoplasmic K^+ rather than cell-wall K^+, based on the rate of exchange and the fact that an analogous compartment for Na^+ was not observed. The fast fraction had an apparent half-time of about 0.5 hour and a rate coefficient of about 1.3 hr.$^{-1}$. Efflux of K^+ from protoplasm to sea water was estimated by multiplying the rate coefficient by the K^+

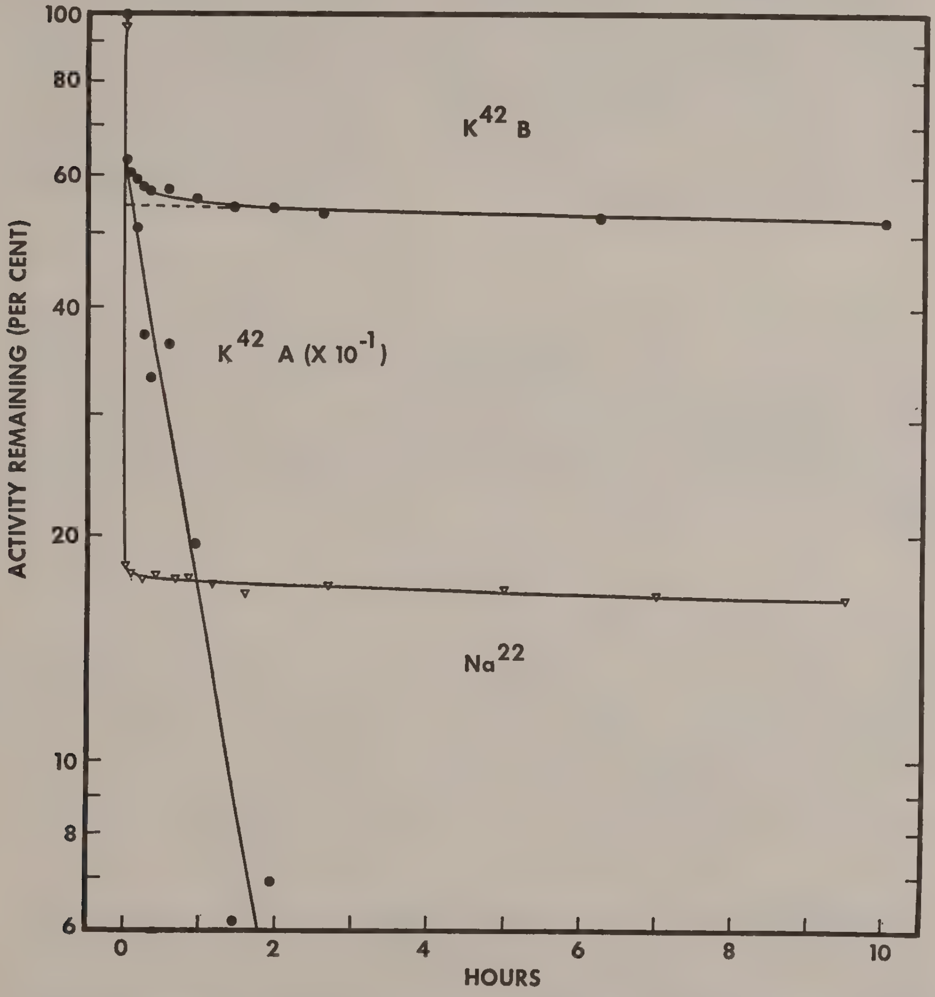

FIGURE 1. Efflux of Na^{22} and K^{42} from cells of *V. ventricosa,* previously labeled for 5 hours (Na^{22}) or one hour (K^{42}) in the light. Rapidly exchanging fraction of intracellular K^{42} (K^{42} A) was obtained by subtracting the extrapolated portion of the slow fraction (K^{42} B) from the total activity. Each point represents a measurement of 11–30 cells.

concentration of the protoplasm (about 13×10^{-8} M/cm².), which gave a value of about 50 $\mu\mu M$/cm². sec.

The K^+ flux from protoplasm to sea water, the rate coefficient, and the apparent size of the protoplasm compartment are all underestimated, however, by the graphical analysis of the washing-out curve (Fig. 1). The error is caused by the series arrangement of protoplasm and vacuole, the relatively small size of the protoplasm compartment, and the similarity between the fluxes across plasmalemma and tonoplast (see Solomon, 1960; Huxley, 1960). First, the protoplasm loses radioactivity to both vacuole and sea water during the washing-out process. Second, the specific activity of the protoplasm after several hours in a K^{42} medium is probably not equal to the specific activity of the medium, but is at a quasi-steady level below that of the medium.

DISCUSSION

The occurrence and direction of any active transport processes in *V. ventricosa* can be determined from a knowledge of the ion concentrations and electric potentials under steady-state conditions. Active transport is indicated by any large differences between the electrochemical potentials of an ion in sea water, cytoplasm, or sap. The difference in electrochemical potential can be estimated by comparing the measured membrane potential with the Nernst equilibrium potential, *i.e.*, the potential at which the ion would be in passive flux equilibrium between the two phases.

$$E_j = \frac{2.3RT}{zF} \log \frac{C_1}{C_2}$$

E_j is the equilibrium potential, C_1 and C_2 are the ion concentrations on either side of the membrane, z is the algebraic valency, and R, T, and F have their usual meanings. In the discussion which follows, the sign of the potential will always be that of the cytoplasm. The sea water and vacuole are taken as ground for the potentials across the plasmalemma and tonoplast, respectively.

Possible active transports of Na^+ and K^+ in *V. ventricosa* may be tested by using the Nernst equation, because these ions are in an approximately steady-state (Table II). Equilibrium potentials for Na^+ and K^+ across plasmalemma and tonoplast are shown in Table III. Also shown are the differences, ΔE, between the measured potential and the equilibrium potential for each ion. The magnitude of the ΔE indicates the relative driving force acting on the ion. The sign of the ΔE, along with the valency of the ion, indicates the direction of that driving force. The large values for ΔE_{Na} at the plasmalemma (−136 mv), and for both ΔE_{Na} and ΔE_K at the tonoplast (−90 and −97 mv) indicate active transport of these ions. An active efflux of Na^+ from protoplasm to sea water and active transports of both Na^+ and K^+ from protoplasm to vacuole are indicated. An active influx of K^+ at the plasmalemma is likely, although the ΔE_K at this membrane is relatively small (+21 mv).

Where marked deviations from flux equilibrium occur, as with Cl^- (Table II), the flux-ratio equation of Ussing (1949) and Teorell (1949) may be used to test

TABLE III

*Equilibrium potentials for Na^+ and K^+ across plasmalemma and tonoplast**

Ion	Plasmalemma		Tonoplast	
	E_j**	$\Delta E = E_{obs} - E_j$	E_j**	$\Delta E = E_{obs} - E_j$
Na^+	+65	−136	+2	−90
K^+	−92	+21	+9	−97

* Calculated from data in Table I.

** $E_j = \frac{-2.3RT}{zF} \log \frac{C_i}{C_o}$ millivolts.

for passive, independent, ion movement.

$$\frac{M_i}{M_o} = \frac{C_o}{C_i \exp(zFE/RT)}$$

M_i/M_o is the predicted flux ratio (influx/efflux), E is the measured vacuole potential, and the other symbols have the same meanings as before. Close agreement between predicted and measured flux ratios is strong evidence for passive ion movement. Discrepancies suggest, but do not prove, active transport, since such passive processes as exchange diffusion and single-file diffusion can cause deviations from the predicted flux ratios (see Ussing, 1960, p. 49).

Measured and predicted flux ratios for Na^+, K^+, and Cl^- between sea water and vacuole are shown in Table IV. The predicted values were calculated from the average vacuole potential of +17 mv and the sap and sea-water concentrations shown in Table I. The large differences between the measured and predicted values for both Na^+ and K^+ support the earlier indications of active efflux of Na^+ and active influx of K^+. On the other hand, the close agreement between the predicted and measured flux ratios for Cl^- (1.70 and 1.79) indicates that Cl^- uptake into the vacuole of growing cells is a passive process.

The absence of active transport of Cl^- from sea water to vacuole, however, does

TABLE IV

Measured and predicted flux ratios for Na^+, K^+, and Cl^- between sea water and vacuole

Ion	Influx/Efflux, M_i/M_o	
	Measured*	Predicted**
Na^+	1.10	5.78
K^+	1.03	0.01
Cl^-	1.70	1.79

* Calculated from data in Table II.

** $\frac{M_i}{M_o} = \frac{C_o}{C_i \exp(zFE/RT)}$.

not preclude the possibility of some active uptake of Cl^- into the protoplasm at both membranes. The predicted flux ratio at the plasmalemma (M_{oc}/M_{co}) is about 0.3, and the predicted flux ratio at the tonoplast (M_{cv}/M_{vc}) is about 6. The actual flux ratios are not known, but the measured value of 1.7 between sea water and vacuole (M_{ov}/M_{vo}) sets an upper limit on the flux ratios. A lower limit of about 1 is set by the experimental conditions, *i.e,* growing cells which maintain a constant Cl^- concentration inside. Thus, the actual flux ratios at plasmalemma and tonoplast must be 4–6 times higher and lower, respectively, than the predicted flux ratios. This suggests either that there is active uptake of Cl^- into the protoplasm at both membranes or that the estimated Cl^- concentration in the protoplasm is too high. The latter possibility is more likely, because either contamination by sap or the presence of minute sap-filled vesicles in the protoplasm (see Buvat, 1963; Sutcliffe, 1962) could raise the estimated Cl^- concentrations above the equilibrium level. Two other possible sources of error are the ion selectivity of the chloroplasts and any changes in the cytoplasmic potential with age.

Valonia ventricosa differs from other plant cells by not showing active uptake of Cl^- into the vacuole. Active Cl^- absorption occurs, for example, in the marine algae *Rhodymenia, Halicystis,* and *Gracilaria* (MacRobbie and Dainty, 1958b; Blount and Levedahl, 1960; Gutknecht, 1965a). In giant characean cells, as well as in roots, storage tissues, and leaves of higher plants, an inward Cl^- or anion pump is essential for maintaining the high salt content of the vacuole (see Dainty, 1964). In *V. ventricosa,* however, Cl^- appears to follow passively while Na^+, and especially K^+, are pumped into the vacuole. Thus, the hypertonicity of the cell interior, which is essential for the growth and expansion of all walled cells (see Rothstein, 1964), is primarily due to an inward transport of cations rather than anions. In this respect *Valonia* resembles yeast and bacteria more than other algae and higher plants.

Active transport of one or more ions from cytoplasm to vacuole is necessary for osmotic reasons, summarized recently by Tosteson (1964). Otherwise, unless the tonoplast were pressure-resistant, the protoplasm would be osmotically unstable toward the sap. For this and other reasons the inward Cl^- pump in both *Halicystis* and *Nitellopsis* was sited at the tonoplast (Blount and Levedahl, 1960; MacRobbie and Dainty, 1958a). In *Nitella* it appears that Na^+ is pumped in at the tonoplast, whereas K^+ and Cl^- are in equilibrium between cytoplasm and sap (Spanswick and Williams, 1964). In *V. ventricosa,* however, it is primarily K^+ which is pumped from cytoplasm to sap.

The energy requirement for K^+ transport in *V. ventricosa* is of interest because of the rapid influx of K^+ (89 $\mu\mu M/\text{cm}^2$. sec.) and the large electrochemical potential gradient against which K^+ is pumped (about 2500 cal./M). The cells in which K^+ fluxes were measured contained about 5×10^{-4} g. protoplasm cm^2. The energy requirement is thus about 1.6 cal./g. protoplasm per hour, which is rather high and suggests that part of the K^+ fluxes may be due to a mediated, but not active, process. such as exchange diffusion (see Ussing, 1960).

The large potential across the tonoplast is another unusual feature of *V. ventricosa.* The marine alga *Halicystis ovalis* and root hair cells of *Avena* show no potential across the tonoplast (Blount and Levedahl, 1960; Etherton and Higinbotham, 1960). Fresh-water Characeae show either no potential or very small potential (Walker, 1955; Kishimoto, 1959; Nagai and Kishimoto, 1964; Findlay and Hope, 1964; Spanswick and Williams, 1964).

At the plasmalemma, both the large negative potential and the active extrusion of Na^+ are features common to many cells. Two other marine algae, *Halicystis* and *Porphyra,* show cytoplasmic potentials of −80 and −42 mv, respectively (Blount and Levedahl, 1960; R. W. Eppley, personal communication). In fresh-water algae and higher plants the plasmalemma potentials are usually somewhat larger (Walker, 1955; Umrath, 1956; Findlay and Hope, 1964; Spanswick and Williams, 1964). Finally, the outward transport of Na^+, possibly coupled with an inward transport of K^+, occurs at the outer plasma membrane of many plant and animal cells (see Dainty, 1962, 1964).

The suitability of *Valonia* for salt-transport studies is questioned by Steward

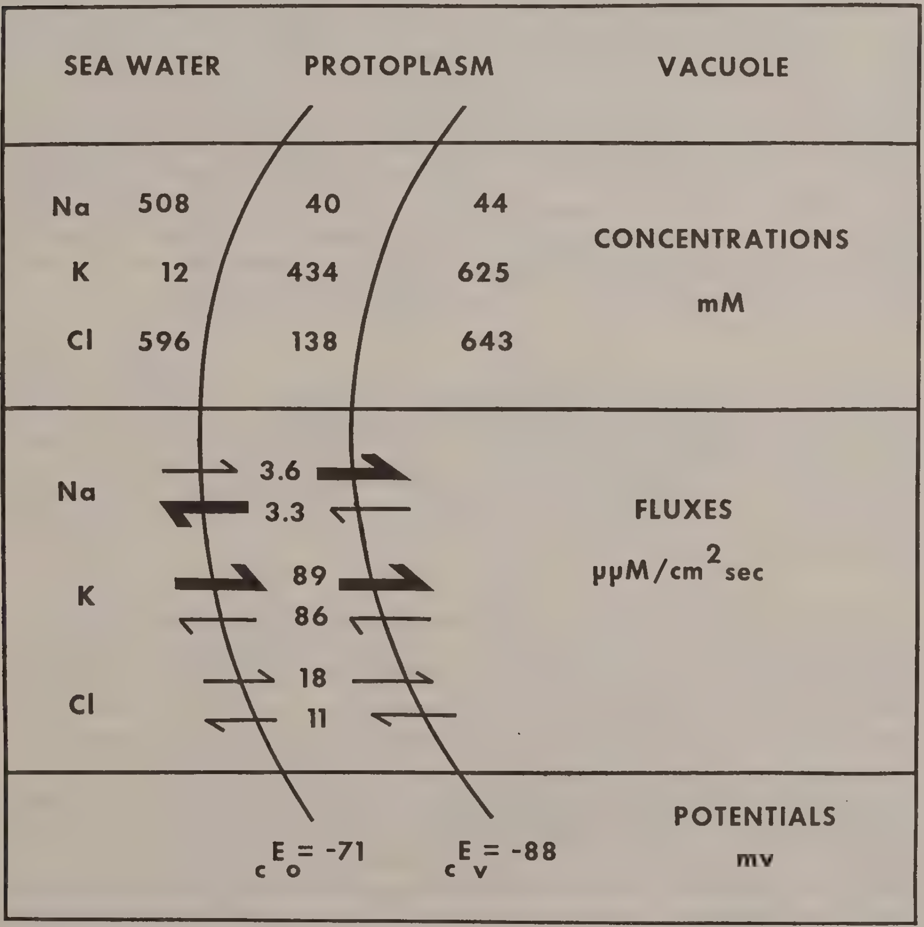
SEA WATER
PROTOPLASM
VACUOLE
Na 508 40 44
K 12 434 625
Cl 596 138 643
CONCENTRATIONS
mM
Na
3.6
3.3
K
89
86
Cl
18
11
FLUXES
μμM/cm² sec
POTENTIALS
mv
$_cE_o$ = -71
$_cE_v$ = -88

Figure 2. Ionic relations in *V. ventricosa.* Provisional scheme showing concentrations, fluxes, and potentials. Large arrows indicate active transport.

and Sutcliffe (1959, p. 289), because the sap is not subject to rapid changes in composition, and because the cells grow slowly and only from aplanospores which send rhizoidal processes into the substratum, *e.g.,* marble chips. They suggest that the rhizoidal processes, as well as the small hapteron cells on the surface of the main vesicle, may be the functional absorbing organs. My results indicate that neither the rhizoidal cells, nor the substratum, nor the hapteron cells are necessary for fairly rapid growth and rapid ion movements. The growth rate of 0.5–1.5% per day in fairly large cells (60–110 mg.) is comparable with that in some other marine algae under fairly similar conditions (Gutknecht, 1965b), and the fluxes of ions across the surface of the main vesicle are more rapid than in most other plant and animal cells. That the sap is not subject to rapid changes in composition is probably due mainly to the large volume:surface ratio.

A provisional scheme of the ionic relations in *V. ventricosa* is shown in Figure 2. The important differences between *V. ventricosa* and other vacuolated plant cells are (1) the absence of active transport of Cl^- into the vacuole, (2) the inward transport of both Na^+ and K^+ at the tonoplast, and (3) the large potential across the tonoplast. Two features of *V. ventricosa* that are similar to other vacuolated plant cells, as well as to plant and animal cells in general, are (1) the active efflux of Na^+ and probably active influx of K^+ at the plasmalemma, and (2) the large negative potential of the cytoplasm relative to the external solution. Thus, the main differences between *Valonia* and other plant cells lie at the vacuole membrane. These results may therefore support the view of Steward (1939) and Steward and Sutcliffe (1959), based on morphological evidence, that the vacuole of *Valonia* and its relatives is not homologous to the vacuole of most other plant cells.

I thank Drs. Felice Aull, Robert Blount, and Douglas Wolfe for helpful suggestions and Dr. Daniel Tosteson for reading the manuscript. I thank Dr. John W. Moore for the use of his electrode puller, Dr. C. P. Hickman for the use of his osmometer, and Dr. Luis Almodovar for supplies of *Valonia.* This research was supported by the U. S. Fish and Wildlife Service and U. S. Atomic Energy Commission.

SUMMARY

1. The marine alga *Valonia ventricosa* regulates its ionic content by means of several ion pumps. An active extrusion of Na^+ and probably an active uptake of K^+ occur at the plasmalemma. At the tonoplast there is an inward transport of Na^+ and especially K^+. The evidence for these ion pumps is that Na^+ efflux at the plasmalemma and Na^+ and K^+ influx at the tonoplast occur against large electrochemical gradients under steady-state conditions.

2. Ion distribution and membrane potentials across plasmalemma and tonoplast were measured. The ion concentrations were: Na^+ 508, K^+ 12.1, and Cl^- 596 m*M*/liter sea water; Na^+ 40, K^+ 434, Cl^- 138 m*M*/liter protoplasm water; Na^+ 44, K^+ 625, Cl^- 643 m*M*/liter sap. The resting potential across the plasmalemma was about 71 mv, cytoplasm negative to sea water. The potential across the tonoplast was about 88 mv, cytoplasm negative to sap. The large potential across the tonoplast is a feature not found in other vacuolated plant cells.

3. Ion fluxes between sea water and vacuole were measured in growing cells of *Valonia*. The fluxes were: Na^+ 3.3–3.6, K^+ 86–89, Cl^- 11–18 $\mu\mu M/cm^2 \cdot sec$. The ratio of influx:efflux for Na^+ and K^+ was close to unity, whereas the flux ratio for Cl^- was 1.70. The latter value is close to that predicted by the Ussing-Teorell equation for a passively moving ion, which suggests that *Valonia*, unlike other vacuolated plant cells, does not actively transport Cl^- into the vacuole.

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Observations on "Milky Water" in Chesapeake Bay

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ABSTRACT: Detached masses of the green alga *Ulva*, or sea lettuce, are often concentrated in shallow water along shorelines, where they decompose. Products of decomposition cause a condition termed "milky water" characterized by a nearly opaque cream color, low oxygen concentrations, and formation of hydrogen sulfide. These conditions are potentially lethal to marine animals, and create unpleasant odors of hydrogen sulfide which may have detrimental chemical activity with some paint pigments.

Sea lettuce, *Ulva lactuca*, is a common marine alga occurring in great quantities in many areas of Chesapeake Bay. The plant has a single, bright green leaf, composed of two cell layers, with a small stalk and holdfast. Reproduction is asexual by the production of four to eight quadriflagellate zoospores in each sporangial cell, or sexual by the dioecious production of biflagellate anisogametes (Taylor 1957). *Ulva* generally occurs in shallow water, where sunlight is adequate for photosynthesis.

During the seasonal cycle of growth and reproduction, the plants may become detached and drifting, especially during the fall, and large masses may be concentrated along shores by the action of tides and wind. Decomposition of this material can cause local areas of "milky water", characterized by the production of hydrogen sulfide, low dissolved-oxygen levels, and nearly opaque, cream-colored water. Such conditions are potentially lethal to small fish and other estuarine fauna. I have found no references to this phenomenon in the literature, but conversations with watermen and others indicate that it is not uncommon in the Chesapeake Bay region and other areas of the Atlantic Coast.

The purpose of this note is to establish the occurrence of milky water from the decomposition products of *Ulva* in Chesapeake Bay, and to point out the potentially lethal conditions for estuarine fauna that result.

An occurrence of milky water was brought to my attention on 15 October 1965, when a large, white patch of water was observed on the west side of Benoni Point, near the confluence of the Tred Avon and Choptank Rivers on Maryland's eastern shore of Chesapeake Bay. The area was permeated with the odor of "rotten cabbage." Water samples were obtained throughout the region, both in milky water and in the surrounding clear water areas, on 18 October 1965, and analyzed at the Bureau of Commercial Fisheries Biological Laboratory, Oxford, Md. Dissolved-oxygen concentrations (standard Winkler method) in clear water samples averaged 11.0 ppm., whereas milky water samples were as low as 4.1 ppm. Dissolved-oxygen values were lower in more opaque, white colored water samples. A strong odor of hydrogen sulfide was evident both in the region of milky water and along the shore, where great quantities of decomposing *Ulva* were piled up in thick windrows (Fig. 1). In the most intensely discolored areas, extending in two separate patches of about 3 to 4 acres each, objects lowered into

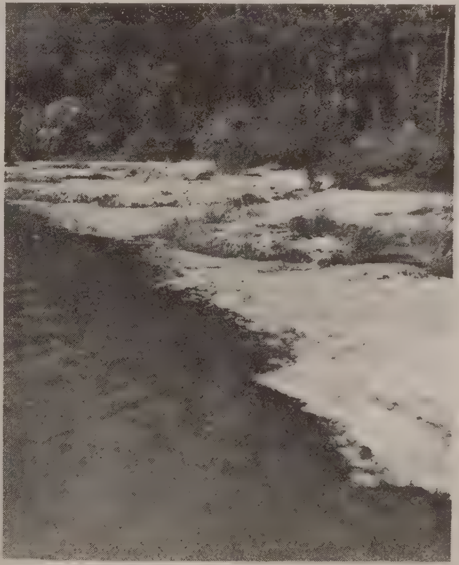

Fig. 1. Windrows of decomposing *Ulva*, concentrated on and near shore by wind and tidal action.

the water could not be seen below 5 or 6 inches. Adjacent clear water had good visibility to depths of 3 to 6 feet. Acetone extracts (Carritt and Carpenter 1951) of the green pigment chlorophyll *a* were low (about 0.6 micrograms per liter) both inside and outside the discolored patches, and were comparable with present and past samples obtained throughout the region in the fall (Hanks 1964).

Centrifuged samples (20 minutes at 2,000 rpm) revealed no concentrations of particulate matter as a cause for water discoloration, and simple iodine tests for starch were negative. Possibly the milky white color is caused by soluble storage or decomposition products of the algal cells. Sampling and further chemical analyses were suspended with the disappearance of the milky water on 21 October 1965.

Although I did not see any fish kills, watermen in the area reported that during establishment of milky water patches, which required about 3 hours, many small fish (probably *Fundulus* or *Menidia*) were moribund and floating on the surface, where flocks of sea gulls were feeding on them. The entire period of milky water lasted about 7 days.

Other instances were reported over the next 2 weeks, however, when irate home owners called the local Department of Agriculture Extension Service and the Bureau of Commercial Fisheries Biological Laboratory to ascertain the cause of unpleasant odors and discolored house paint. The latter is generally attributable to the conversion of white zinc oxide, a common pigment in exterior house paints, to black zinc sulfide by the high concentrations of hydrogen sulfide.

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Ser. 13, vol. viii, p. 177, March, 1965.

ANTONBRUUNIA VIRIDIS, A NEW INQUILINE ANNELID WITH DWARF MALES, INHABITING A NEW SPECIES OF PELECYPOD, *LUCINA FOSTERI*, IN THE MOZAMBIQUE CHANNEL.*

By Olga Hartman† and Kenneth J. Boss.‡

Two interesting non-related phenomena are illustrated by a new dioecious polychaetous annelid, which does not ally itself with any of the existing families, but is most nearly related to species of the small family Pilargidae. One of these is sexual dimorphism in which the males are dwarfs and the other is an apparent obligatory inquilinism of the two members of a sexual pair in which a third individual of either sex is generally excluded. Both phenomena are known separately in a few other polychaetes, but neither is common, and their occurrences, where known, are not phylogenetically related. This species of annelid inhabits the mantle cavity of a new species of the eulamellibranch genus, *Lucina*.

The collection was taken by the authors on board the National Science Foundation's Research Vessel, ' Anton Bruun ', during Cruise 7 of the International Indian Ocean Expedition. The authors are indebted to the staff of Cruise 7 and to the coordinator of the expedition's biology programme, Dr. John Ryther. They also wish to acknowledge the support of the National Science Foundation for permission to participate in the cruise.

Description of the Polychaete.

Antonbruunia viridis, new genus and new species.
(Figs. 1–5).

The holotype (female) of *Antonbruunia viridis* is in the collection of the Allan Hancock Foundation, University of Southern California, Los Angeles, California. Paratypes are also deposited in the United States National Museum. The type locality is Station 364 C, R/V ' Anton Bruun ', Cruise 7, International Indian Ocean Expedition, 23° 20′ S; 43° 36·3′ E, N.W. of Tuléar, Madagascar, in 39–45 fathoms (68–82·3 metres). The animals were collected with a modified Agassiz trawl and were found in sediments of black-brown oozy mud and detritus. The living contents of the sample consisted chiefly of a small lucinoid clam numbering more than 100 specimens.

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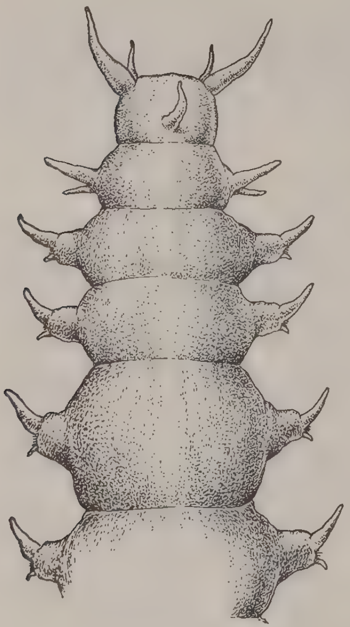
Figs. 1–5.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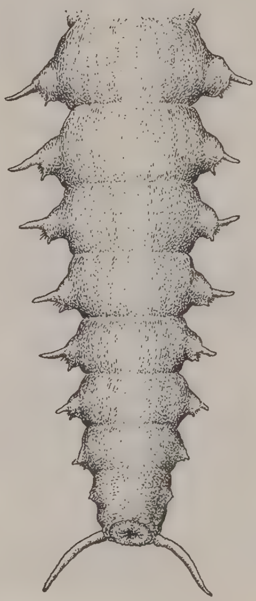
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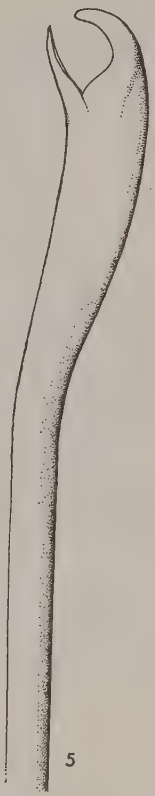
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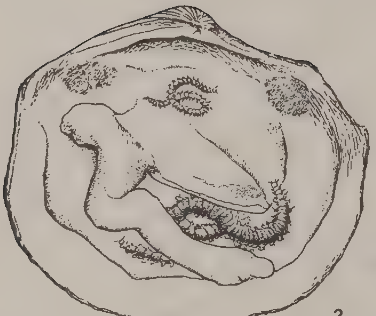
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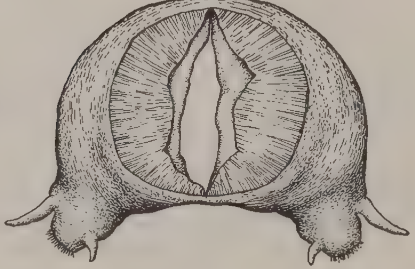
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Fig. 1. Dorsal view of the anterior end and first 5 segments of female of *Antonbruunia viridis* (×5·7). Fig. 2. Dorsal view of the posterior end with the body segments and pygidium of female of *Antonbruunia viridis* (×5·7). Fig. 3. Male and female specimens of *Antonbruunia viridis* in situ with the right valve and mantle of the mollusk removed (×4·1). Fig. 4. Cross section through a postmedian segment of the body of female of *Antonbruunia viridis* (×5·7). Fig. 5. Lateral view of a neuropodial seta from a postmedian parapodium of *Antonbruunia viridis*, enlarged.

Antonbruunia is established in honour of the distinguished Danish marine biologist, Anton Bruun, after whom the research vessel was named. The specific name, *viridis*, refers to the green colouration of the polychaete.

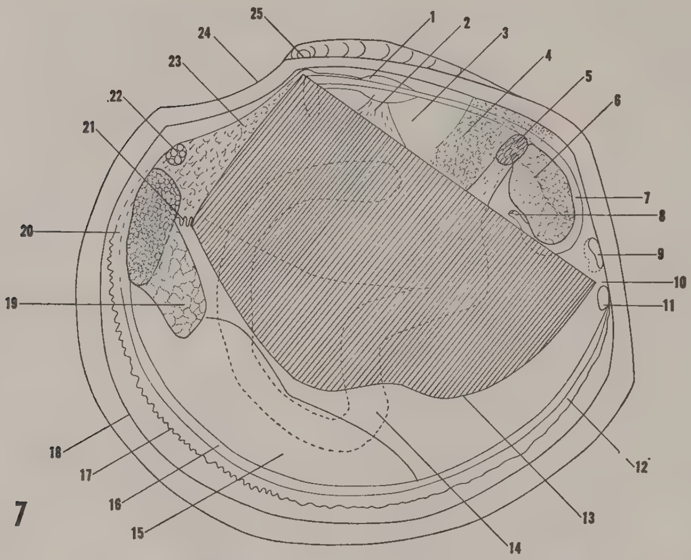
Description. On opening the clam and laying aside the mantle, the pink gills are exposed. The conspicuously green and white banded, vermiform body of the female polychaete is usually in such a position that the oral end is directed towards the siphons of the host clam and the body is coiled about the long, pedal extension of the clam. The much smaller male is less easily detected and generally is near the umbonal region of the clam; its anterior end is also directed towards the siphons. About 80 per cent of the molluscs examined contained a pair of the polychaetes, with two dimorphic individuals in approximately the position indicated. In one instance, a third individual of the commensal was encountered; it was intermediate in size and colourless and thus resembled the male.

The female measures 14 mm. long by 0·7 mm. wide and has about 52 segments. The body is terete, somewhat depressed, widest near the middle, and tapers in either direction. In life it is brilliant light green but the segmental grooves and parapodia are chalky white. Some green colour is retained subsequent to preservation but the chalky whiteness is dimmed. The cuticle is smooth and glistening. The male is pale to white and lacks the green pigment. Its size is less than half that of the female and it possesses about half to two-thirds the number of segments of the female. Cephalic, parapodial and anal structures are proportionately like those in the female.

The prostomium is directed forward and is trapezoidal in shape. It is wider than long, narrowest in front, and lacks eyes. A pair of cirriform antennæ is inserted at the frontoectal margins and a similar, though smaller, pair is located ventrolaterally (normally not seen in dorsal view). A median antenna, resembling those at the front, is inserted posteriorly on the dorsal surface of the prostomium (fig. 1). The pharynx, partly everted in some individuals, is cylindrical and short. It lacks jaws and terminates distally in a few widely spaced short papillæ. The retracted proboscis is limited to the first two segments.

The first segment or peristomium is a complete ring, slightly longer than the second. It lacks parapodia and has two pairs of tentacular cirri on either side. The dorsal pair of cirri are longer than the ventral pair and slightly larger than the dorsal cirri of more posterior segments. The second segment is the first setigerous one; it resembles the more posterior segments but is less developed. The third segment is similar to the first but has paired pigment patches and contains ova, as do the other more posterior segments. The size of the parapodia increases gradually to the postmedian region where they become progressively smaller. All parapodia are subbiramous but appear uniramous. The notopodia are represented only by a dorsal cirrus and a slender embedded notoaciculum which is straight and distally pointed. Neuropodia are well-developed

Figs. 6–9.



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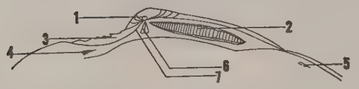

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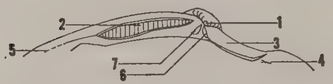

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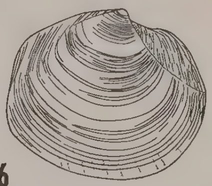

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Fig. 6. External view of the right valve of the holotype of *Lucina fosteri* (length = 12·9 mm.).

Fig. 7. Anatomical diagram of *Lucina fosteri* with the left valve and mantle removed (length = about 12 mm.). 1. Ventricle. 2. Auricle. 3. Pericardium. 4. Kidney. 5. Posterior pedal retractor muscle. 6. Posterior adductor muscle with 'quick' and 'catch' fibres. 7. Rectum. 8. Anus. 9. Exhalant aperture with invaginated siphon. 10. Inter-siphonal septum. 11. Inhalant aperture. 12. Point of fusion of middle lobes. 13. Ctenidium. 14. Foot. 15. Mantle fold. 16. Inner lobe of the mantle. 17. Middle lobe of the mantle. 18. Outer lobe of the mantle. 19. Anterior adductor muscle with 'quick' and 'catch' fibres. 20. Point of fusion of mantle lobes. 21. Labial palps. 22. Anterior pedal retractor muscle. 23. Digestive diverticula. 24. Shell edge. 25. Umbo.

Fig. 8. Internal view of the right valve of *Lucina fosteri*.

Fig. 9. Internal view of the left valve of *Lucina fosteri*. (Length = about 10 mm.). 1. Umbo. 2. Ligament. 3. Lunule. 4. Anterior lateral tooth. 5. Posterior lateral tooth. 6. Anterior cardinal tooth. 7. Posterior cardinal tooth.

and are directed laterally in the anterior region. More posteriorly they become more ventrally located (fig. 4) so that the members of a pair appear to be modified for attachment to the tissues of the host clam. Both presetal and postsetal lobes are short, broad, and distally truncated. About 26–30 short yellow setæ emerge in compact transverse series and are arranged in three transverse rows. They are supported by two slender, distally pointed, completely embedded acicula. All setæ are similar; they are simple and yellow with a long, straight shaft which is distally bifid, with the larger tooth sharply falcate and the shorter secondary tooth nearly straight (fig. 5). These setæ are so thick and robust that those in a fascicle are separated with difficulty. The posterior end of the body terminates in a pair of lateral cirriform processes (fig. 2).

Remarks. *Antonbruunia viridis* is closely allied to the Pilargidae in having a simple prostomium, a peristomium with paired tentacular cirri, and setæ which are entirely simple (Hartman 1947). It differs from the Pilargidae in having nearly uniramous rather than biramous parapodia, in lacking eyes but possessing paired antennæ on the prostomium, and in being sexually dimorphic. *Antonbruunia* seems, therefore, to be modified for a commensal rather than a free-living existence.

Disparity in sizes of the sexes is known in a few other polychætes. *Ophryotrocha puerilis* Claparede and Metchnikoff, a member of the Dorvilleidae exhibits a type of protandry in which all individuals are small males, up to the 12- or 20-segmented stage. Thereafter, to the 28–34 segmented stage they become females and remain so unless starved, in which case they revert to the male condition; or, if amputated to a few (2–10) segments, they again assume the male phase (Hartmann and Huth, 1936). Sex reversal may be effected by the addition of egg extract, when females become males. Whether sex reversal is typical of *Antonbruunia viridis* is not yet known.

Small, perhaps dwarf male individuals have been reported in a spionid, *Polydora commensalis* Andrews (1891), commensal with a hermit crab inhabiting dead shells of a nassid snail overgrown with the hydroid, *Hydractinia*. The polychaete occupies the columella of the shell, through which it constructs a tunnel. When the crab moults and leaves the shell, the worm also leaves, but remains with the crab until another suitable shell is found, which both then enter. A small, perhaps male individual has been observed in the apex of the nassid shell.

The association of polychaetes with other animals is not rare; the literature has been partly reviewed by Clark (1956). Certain genera in some families are almost totally inquiline or parasitic. Such are polynoid genera *Acholoe*, *Alentiana*, *Arctonoe*, *Hesperonoe*, *Malmgrenia*, *Polynoe*, *Scalisetosus*, and some species of *Halosydna*, *Harmothoe*, *Gattyana*, *Lepidasthenia*, and others. *Hipponoe*, with the barnacle, *Lepas*, and *Benthoscolex*, with holothurians, are known in the Amphinomidae. Most species of *Spinther* in the Spintheridae are associated with sponges. *Haplosyllis* and *Calamyzas*, representing the Syllidae, are generally regarded as symbionts. Several genera of Hesionidae are known to be commensal; *Ophiodromus* occurs with echinoids, *Hesionella* with *Lumbrineris*, and *Parasyllidea* with *Tellina*. The genera *Nereis* and

Cheilonereis in the Nereidae are partly inquiline. The Arabellidae have several parasitic genera including *Labidognathus*, *Labrorostratus*, and *Oligognathus*. In the Lysaretidae, *Iphitime* is parasitic, and, in the Flabelligeridae, several species occur only with certain echinoderm hosts. More complete references to these genera are in Hartman (1959).

Molluscs which are hosts to polychaetes are known chiefly from those instances where damage is done to the shells. Several species of *Polydora* (Spionidae) attack the calcareous shells and cause mud blisters. Some chitons, limpets, and large snails have occasional commensals, such as polynoids, nereids and eunicids. The hesionid *Parasyllidea humesi* Pettibone (1961) was found in the mantle cavity of *Tellina nymphalis* Lamarck.

Description of the Mollusc.

The host mollusc of *Antonbruunia viridis* has hitherto remained undescribed and unnamed. The following is a characterization of the bivalve with some remarks on its anatomy and its specific affinities.

Lucina fosteri, new species.

(Figs. 6–9.)

The holotype of *Lucina fosteri* is in the collection of the Division of Mollusks of the United States National Museum, catalogue number 654276. Paratypes are also deposited in the United States National Museum and the Allan Hancock Foundation. The type locality is the same as that of *Antonbruunia viridis*. This species is named in honour of the late Mr Richard Winslow Foster, long associated with the Department of Mollusks at the Museum of Comparative Zoology at Harvard University.

Description. Shell medium to small (fig. 6), reaching a length of 14–15 mm., and a height of 11–12 mm., suborbicular in outline, rather compressed with the left valve slightly more inflated. Nearly equilateral and equivalve, rather thin, translucent, and fragile. No gaping in the valves. No posterior flexure. Umbos nearly central, strongly prosogyrous, inflated, slightly elevated; umbonal cavity well-developed. Anterior dorsal margin concave, marking the extent of the lunule, sharply separated from the anterior margin which is broadly rounded and coextensive with the gently convex ventral margin. Posterior dorsal margin straight to weakly convex. Posterior margin straight, giving the outline of the shell a marked, broad posterior truncation. Sculpture concentric, consisting of regularly spaced raised lirations (about 5 per mm.) which are obsolete on the disc and which tend to become stronger or more lamellose peripherally, particularly on the anterior and posterior slopes. Central disc almost smooth. Extremely fine, irregular radial incisions rarely evident on the disc. Three to six concentric growth rings. Weak anterior and posterior ridges radiating from the unbo and delimiting the anterior dorsal and the posterior dorsal areas or slopes. Anterior ridge more sharply defined and somewhat convex; posterior ridge more or less straight and delimiting the union of the posterior and ventral margins. Ligament yellowish-brown, strongly developed, partly internal, and somewhat sunken in a long, narrow, lanceolate escutcheon. Lunule well-developed but not deeply impressed, stronger in the left valve and not sculptured. Entire hingement rather weak, except for the strong ligament. Dentition of the right valve (fig. 8) consisting of lateral and cardinal elements, both nearly obsolete. Remnants of anterior and posterior lateral teeth present; anterior lateral tooth stronger than the posterior and located beneath the anterior extremity of the lunule; posterior lateral tooth consisting of a mere vestige posterior to the end of the escutcheon. Cardinal dentition consisting of a posterior or bifid cardinal tooth on the cardinal plate beneath the umbo and of an anterior cardinal tooth coalesced with the ventral margin of the lunule. Dentition of the left valve (fig. 9) more obsolete than that of the right. Both anterior and posterior lateral teeth vestigial; anterior lateral tooth a mere thickening beyond the end of the lunule; posterior lateral tooth consisting of nothing more than a crease-like extension of the nymph. Cardinal dentition consisting of an anterior bifid tooth coalesced marginally with the edge of the lunule and of a single narrow, diverging posterior tooth. No true internal ribs, but numerous radial vermiculations internally; internal edge of the shell not denticulate. Muscle scars poorly impressed. External colour apricot centrally and umbonally, weakening peripherally. Internal surface shining, predominantly apricot with central concentration of colouration.

Length	Height	Width	
12·9 mm.	11·0 mm.	05·6 mm.	Holotype
11·4 mm.	10·3 mm.	05·0 mm.	Paratype
10·8 mm.	09·9 mm.	05·0 mm.	Paratype
10·8 mm.	09·6 mm.	04·8 mm.	Paratype

Remarks. Figure 7 illustrates the general anatomy of the species. The mantle possesses three distinct lobes: a broad outer lobe, the entad surface of which gives rise to the periostracum: a narrow, middle lobe, which is irregularly undulate anteroventrally and which fuses postero-ventrally beneath the inhalant aperture; and a thickened inner muscular lobe which fuses posteriorly. The mantle is entirely fused in its dorsal arcuation from the area of the anterior siphonal region to a point immediately dorsad of the exhalent siphon. Antero-ventrally is an extensive pedal gape. A mantle fold consisting of extensive blood sinuses is developed anteroventrally; this may represent an accessory respiratory organ or ' mantle gill '. Exhalent and inhalent apertures are formed posteriorly. The middle lobe of the mantle is fused anterior to the inhalent aperture and the inner lobe of the mantle is fused between these apertures. A muscular complex supporting the siphonal apertures is developed at the intersiphonal septum, formed by the junction of the posterior extremity of the demibranchs and the fusion of the inner mantle lobes. The oval inhalant aperture is simple whereas the slit-like exhalant aperture has an invaginated extensible siphon. There are no sensory papillæ or tentacles. The posterior apertural structures are similar to those of *Lucina chryostoma* (Meuschen) as described by Allen (1958, fig. 9e).

Both adductor muscles are differentiated into ' catch ' and ' quick ' fibres. The anterior adductor has a long posteroventral portion which is separated from the pallial muscle and which forms a shelf across the mantle cavity ventral to the mouth. The surface of this extension is ciliated and forms a sorting tract leading into the mantle cavity. Lucinids possess an anterior inhalent mucoid tube which is constructed by the foot, but none of these tubes were noted when this species was collected. The anterior pedal retractor muscle inserts on the shell dorsal to the anterior adductor. The posterior pedal retractor muscle inserts above the posterior adductor, traverses the kidney, and splays out into the foot.

The extensile foot is long and vermiform with a slight distal expansion. Its proximal portion, or heel, is laterally compressed. The functions of the foot include burrowing, locomotion, and probably the construction of the interior inhalant tube. No byssal gland is evident.

The gills consist of single right and left inner demibranchs which are united posteriorly behind the heel of the foot and which are connected to the viscera dorsolaterally. The flat, homorhabdic demibranchs are extensive and have many closely aligned filaments. The pinkish-red colouration of the ctenidia in life may indicate the presence of hemoglobin in the blood. This respiratory pigment has been observed and studied in *Phacoides pectinatus* (Gmelin) by Read (1962). The flattened lip like palps are much reduced.

The morphology of the viscera has not been studied in detail. The broad, thin-walled auricles are paired and lead directly from the sinoidal connection with the ctenidia to the ventricle which completely envelops the rectum. The rectum contains irregularly compacted facies and terminates in a multilobate anus which discharges into the suprabranchial chamber. The heart lies in an extensive pericardium at the postero-ventral extremity of which are paired ciliated reno-pericardial tubes. The kidney occupies the area between the pericardium and the posterior adductor muscle.

Lucina fosteri exhibits some degree of intraspecific variation in many of its conchological characteristics. Young individuals have a shorter posterior dorsal margin and a less truncated appearance posteriorly. The weak internal radial vermiculations simulate weak marginal denticulations, though the shell is not truly denticulate. The hinge dentition, which is characteristically weak, becomes more obscure in adult or larger specimens. For example, the bifid cardinal tooth of the right valve may lose its bifid aspect and appear as an irregular, subdeltoid protuberance.

The ligament, which is yellowish-brown, consists of a dark outer organic element, a horny basal layer and an inner elastic calcareous portion. Allen (1960) has discussed the structure of the lucinoid ligament in detail.

The shell itself is fragile and, after preservation, is brittle and easily fragmented.

None of the species of lucinids mentioned by Dautzenberg (1929) is closely related to *Lucina fosteri*. The species most closely allied to *L. fosteri* are those described as *Phacoides capensis* and *P. aequalis* by Thiele and Jaeckel (1931) in their report on the bivalves of the *Valdivia* German Deep Sea Expedition. Barnard (1964) in his recent treatment of these species, gave their distribution in South Africa; he further remarked that the two species might well be synonymous. The regularity of the concentric sculpture may be taken as an identifying characteristic which would distinguish both *L. capensis* and *L. aequalis* from *L. fosteri* where the sculpture is stronger peripherally and where the disc is nearly smooth. Further, the posterior truncation of adult specimens of *L. fosteri* is unlike the convexly rounded posterior margin of the *Valdivia* species. Though the colouration of *L. aequalis* is similar to that of *L. fosteri*, the proportion of the valves is not. *Lucina fosteri* is distinctly longer than it is high and the left valve is slightly more tumid than the right. Futhermore, Barnard indicated that both *L. capensis* and *L. aequalis* are allied to the widely distributed *Lucina borealis* (Linnaeus). Anatomically, *L. fosteri* differs from *L. borealis* in that the outer mantle lobe of *L. fosteri* is not fused posteroventrally and the posterior inhalant aperture is not provided with sensory papillæ. An extensive series of the *Valdivia* species would afford an opportunity for anatomical and conchological comparisons which might provide a further basis to distinguish *L. aequalis* and *L. capensis* from *L. fosteri* or, on the other hand, to indicate that each represents a geographically isolated population of a single, more widely distributed species.

The generic characteristics of lucinids were discussed by Chavan (1937–38) who showed that the name '*Phacoides*' is not tenable. Therefore, Dall's (1901) usage of '*Phacoides*' becomes synonymous with *Lucina* as indicated by Chavan. Of the numerous subgenera of *Lucina*, none except *Lucina s. s.* allows for the inclusion of *L. fosteri*. Thus, *L. fosteri* is placed in the nominate subgenus, even though the development of the lateral dentition is poor.

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Observations on Lampreys in the Naknek River System of Southwest Alaska

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Available evidence suggests that both anadromous and dwarfed freshwater forms of the parasitic Arctic lamprey, *Lampetra japonica,* occur sympatrically in the Naknek River system of southwest Alaska. The freshwater form is the more common of the two. Mature, spawning, and spent lampreys of this form are morphologically almost identical with nonparasitic *L. lamottenii.* Spawning of the freshwater form of *L. japonica* occurs in May, June, and early July in many streams throughout the Naknek system. Spawning behavior is essentially the same as that reported for other small lampreys. Ripe and spent anadromous adults have been collected in June, primarily from the Naknek River. Limnetic populations of immature adults are evident in most lakes in July, August, and September. During the same time and continuing into fall, some immature adults migrate downstream from Coville, Grosvenor, and Brooks lakes into Naknek Lake. Transforming ammocoetes are most evident in spring and early summer. Although *L. japonica* parasitizes several species, there is no evidence that parasitism in freshwater is detrimental to any fish population in the Naknek system.

INTRODUCTION

THE Arctic lamprey, *Lampetra japonica* (Martens), is widely distributed throughout lakes and streams of the Naknek River system of southwest Alaska. Observations on lampreys from 1958 to 1964 suggest that most *L. japonica* in this system complete their life cycle in freshwater, while only a few migrate to sea. Originally the mature adult and spawning lampreys of this freshwater form in the Naknek system were believed to be nonparasitic American brook lampreys, *Lampetra lamottenii* (LeSueur), which reportedly occur in Alaska (Wilimovsky, 1954; Hubbs and Lagler, 1958). Available evidence suggests, however, that all lampreys in the Naknek system are parasitic *L. japonica.* This paper discusses the relation between *L. lamottenii* and *L. japonica,* and describes the general temporal and spatial distribution and known biology of lampreys in the Naknek system.

Naknek River, which originates at the outlet of Naknek Lake and flows into Naknek–Kvichak Bay at the northeast corner of Bristol Bay, is 34 miles long. Naknek Lake is the downstream terminal of seven interconnected lakes: Murray, Hammersly, Coville, Grosvenor, Brooks, Idavain, and Naknek (Fig. 1). All of the lakes are glacial in origin, dating from Wisconsin times (Muller, 1952; Karlstrom, 1957). Naknek Lake itself comprises three major basins, Iliuk Arm, North Arm, and South Bay. In addition, there is a shallow outwash plain in the lower end of the lake. Each basin and lake has from one to several lateral tributaries, and most have prominent inlet or outlet streams. Much of the Naknek River system lies within Katmai National Monument.

The first record of lampreys in the Naknek system was the report of adults and ammocoetes of *Entosphenus* sp. (=*Lampetra* sp.) off the mouth of an unnamed creek in Brooks Lake (Greenbank, 1954). Cahalane (1954:88), in an interim report of a biological survey of Katmai National Monument, stated that *Entosphenus* (=*Lampetra*) *tridentatus* (Gairdner) was "reported from Grosvenor Lake." Extensive collecting in Grosvenor Lake in 1961 and 1962 revealed no *Lampetra tridentata*, although *L. japonica* was plentiful. I know of no other report of *L. tridentata* from the Bristol Bay area, although Jordan and Gilbert (1899) reported this form from Unalaska Island in the Aleutian Island chain and gave an unspecified Bering Sea record from a fur seal stomach. Berg (1948) listed a record (addenda to vol. 1, p. 494, of translation) of *L. tridentata* from Bering Island off the Kamchatka Peninsula, and Okada (1960) reported it from the Yûhutu River, Hokkaidô, Japan. In North America *L. tridentata* normally occurs from California to south of the Alaska Peninsula (Evermann and Goldsborough, 1907; Clemens and Wilby, 1961; Shapovalov, *et al.*, 1959).

METHODS

Most lampreys were caught during sampling programs designed to enumerate or sample populations of juvenile sockeye salmon. The most commonly used sampling devices were fyke nets, which were fished in streams and rivers, and tow nets, which were fished in lakes. Additional specimens were caught by hand or with dip nets, seines, or gill nets. Fyke nets proved to be excellent for sampling downstream movements of adults and ammocoetes in streams. Tow nets, 10 ft in diameter, dragged behind two outboard-powered boats, were successful in capturing *L. japonica* in limnetic parts of lakes. Burgner (1958) described the use of these 10-ft tow nets as sampling gear. They were modified from 1-m tow nets used by Johnson (1956).

Trunk myomere counts, tooth counts, and proportional body measurements were made on specimens from throughout the Naknek system. Tooth counts were made on the number of supraoral cusps, infraoral cusps, circumoral teeth, and bicuspid circumorals. Proportional body measurements were taken on the length of tail, depth of body, length of eye, length of snout, length of disk, and length over gill openings. All counts and measurements were taken in the manner described by Hubbs and Trautman (1937). Vladykov (1949) discussed the differences in terminology of lamprey dentition used by various authors. All specimens on which counts and measurements were made were deposited either in the Auke Bay Biological Laboratory Fish Collection or in the Oregon State University Fish Collection.

The lamprey genus *Entosphenus* differs from *Lampetra* primarily by the presence of a row of teeth on the posterior field of the sucking disk (Creaser and Hubbs, 1922). Berg (1948) and Vladykov (1949) referred to these teeth as lower or mandibular labials. Berg listed *E. japonicus* as a synonym of *L. japonica* and apparently regarded *Entosphenus* as monotypic (*E. tridentatus*). Much of the North American lamprey literature considers *Entosphenus* and *Lampetra* as separate genera (Creaser and Hubbs, 1922; Vladykov, 1949; Hubbs and Trautmen, 1937). More recently, however, following Bailey (1951: 190), some authors have considered *Entosphenus* synonymous with *Lampetra* (Walters, 1955; Trautman, 1957).

MERISTICS AND MORPHOLOGY

There are three groups of adult lampreys in the Naknek system; two are commonly found throughout the system, and one is less evident and apparently has a limited distribution (Fig. 1). One of the two principal groups include immature lampreys usually less than 200 mm long that are found pri-

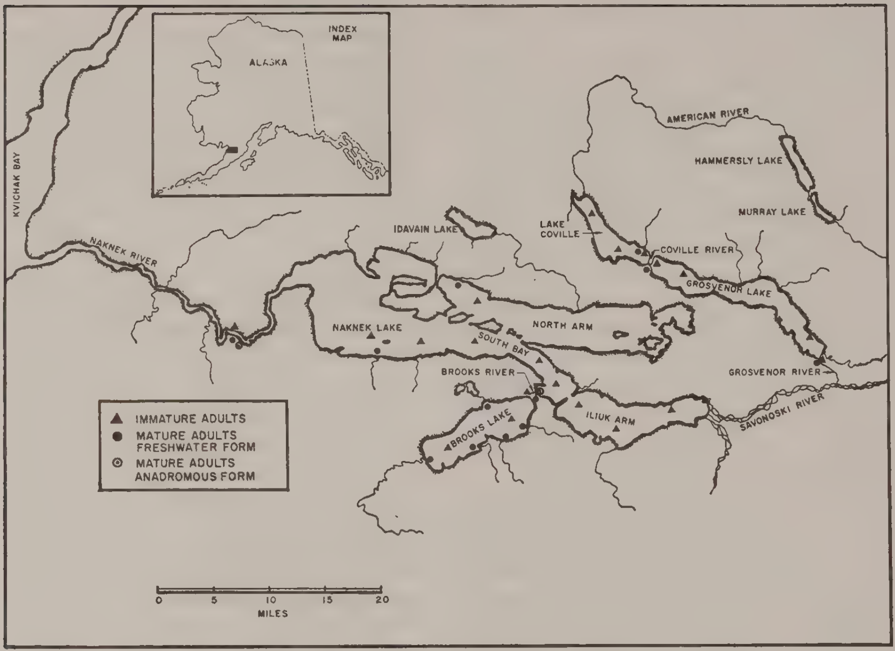
INDEX MAP
ALASKA
KVICHAK BAY
NAKNEK RIVER
IDAVAIN LAKE
LAKE COVILLE
AMERICAN RIVER
HAMMERSLY LAKE
MURRAY LAKE
COVILLE RIVER
GROSVENOR LAKE
NAKNEK LAKE
NORTH ARM
SOUTH BAY
BROOKS RIVER
GROSVENOR RIVER
SAVONOSKI RIVER
ILIUK ARM
BROOKS LAKE
▲ IMMATURE ADULTS
● MATURE ADULTS FRESHWATER FORM
⊙ MATURE ADULTS ANADROMOUS FORM
0
5
10
15
20
MILES

Fig. 1. Naknek River system of southwest Alaska showing locations where *Lampetra japonica* was collected.

marily in the late summer and fall. These lampreys are actively feeding and are frequently seen attached to host fish. Their teeth are usually well developed and robust. Their functional intestine is from three to six mm in diameter and is occasionally distended to 10 mm with food. Gonads of these lampreys are poorly developed (maturity stages 1 to 3 of Vladykov and Follett, 1958). The other principal group consists of mature breeding or spent lampreys less than 200 mm long that are found in the spring and early summer. These lampreys are almost identical with and were initially believed to be nonparasitic *L. lamottenii*, but failure to demonstrate the existence of a nonparasitic lamprey life history in the Naknek system has led me to interpret these as freshwater dwarfed *L. japonica* (*L. j. kessleri* of Berg). Berg (1931: 105, 1948:37) discussed the difficulty of separating mature and breeding specimens of freshwater forms of *L. japonica* from allied nonparasitic forms. The third group also involves mature lampreys in the spring. These are much larger, however, and are believed to be anadromous *L. japonica*. Eight specimens from 219 to 311 mm in total length were collected in the Naknek River, and one specimen 218 mm long was taken at the mouth of Brooks River.

It is not possible to determine morphologically if mature lampreys taken in freshwater are anadromous or freshwater forms. Although size itself is not a definitive measure, Berg (1931:103, 1948:35) has pointed out that mature freshwater *L. japonica* usually do not exceed 200 mm in length, suggesting that the nine mature Naknek system specimens that ranged from 218 to 311 mm and averaged 253 mm in total length are anadromous. The capture of eight of these specimens just at the head of tidewater in the Naknek River and the occurrence of recently transformed immature adults in the same location also suggest that some Naknek system *L. japonica* are anadromous. The genetic or ecological distinctness of anadromous and freshwater populations of *L. japonica* in the Naknek system is not known. These populations may be similar to the somewhat confused discreteness of sympatric anadromous and freshwater populations of sockeye salmon, *Oncorhynchus nerka* (Walbaum), in Cultus Lake (Ricker, 1938).

TABLE 1. SUMMARY OF MERISTIC AND MORPHOMETRIC CHARACTERS OF *Lampetra japonica* FROM THE NAKNEK RIVER SYSTEM.

Character	Immature (N = 69)		Mature: Freshwater Form (N = 74)		Mature: Anadromous Form (N = 9)	
	Range	Mean	Range	Mean	Range	Mean
Supraoral cusps	2–4	2	1–2	2		2
Infraoral cusps	7–11	8.6	5–10	8.2[2]	7–9	8.2
Circumoral teeth	5–7	6.0	4–6	5.9		6
Bicuspid circumorals	4–6	5.8	4–6	5.7		6
Trunk myomeres	66–73	69.5	66–72	69.4	68–72	70.2
Total length (mm)	115–226	166.7	117–188	154.9	218–311	253.3
Length of tail[1]	219–298	271.9	228–319	292.2	256–300	281.8
Depth of body[1]	44–83	58.5	54–100	67.4	62–73	64.0
Length of eye[1]	17–35	26.6	16–30	21.6	16–23	20.9
Length of snout[1]	69–92	79.8	46–93	68.9	75–84	78.7
Length of disk[1]	44–67	55.3	38–57	47.2	45–62	53.1
Length over gill openings[1]	83–109	97.2	88–119	100.7	97–112	103.6

[1] Proportional body measurements expressed in thousands of total length.
[2] Infraoral cusps could not be counted on two specimens.

Meristic and morphometric data were similar in all three groups of Naknek system lamprey (Table 1). All but two specimens had two cusps on the supraoral lamina. These specimens, both apparently anomalous, were a mature freshwater male with only a single median cusp and an immature male with two thin, sharp cusps between the normal ones.

The circumoral tooth series usually contained six bicuspid teeth, although occasionally there were only four or five bicuspid teeth with one or two unicuspid teeth in the series. Infrequently, rather than six there were four, five, or seven teeth in the circumoral series. In the mature freshwater lampreys, two specimens had only four circumorals while one specimen had five. Two immature specimens had seven circumorals and one specimen had five.

Robustness in lamprey dentition is a difficult feature to quantify. Although the immature lampreys generally had sharper and more robust teeth than mature specimens, both groups had successive sets of corneous sheaths over their teeth, and various degrees of the reversal did occur. Lamprey dentition tends to become less robust and blunt during maturation (Hubbs, 1925).

Differences in eye, snout, disk, and tail lengths and in body depth (Table 1) are believed to reflect changes in proportional body structure associated with maturation. In general, relative to total length, eye, snout, and disk lengths of parasitic *Ichthyomyzon* decrease with increased age and maturity, whereas body depth increases (Hubbs and Trautman, 1937). Length progressively becomes smaller in the final maturation of fully grown lampreys (Leach, 1940:30; Vladykov, 1949:13). The average length of immature adult parasitic lampreys could be greater, therefore, than that of mature, spawning, or spent individuals.

The best evidence for the existence of nonparasitic lampreys in the Naknek system would be the presence of metamorphosing ammocoetes with maturing gonads (Hubbs and Trautman, 1937:43) or of not fully mature recently transformed adults with nonfunctional intestines. In nonparasitic lampreys, metamorphosis takes place in late summer and early fall, and the alimentary system rapidly becomes nonfunctional (Hubbs, 1925:587). Although no longer feeding, these lampreys continue to live several months and become fully mature and spawn the following spring. No maturing and metamorphosing ammocoetes or recently transformed adults with nonfunctional intestines have been observed in the Naknek system. Recently transformed adults in this system were all collected in the spring or early summer and had functional intestines, indicating a parasitic life history. Excellent discussions of basic differences in life histories of parasitic and nonparasitic lampreys are given by Hubbs (1925), Hubbs and

Trautman (1937), Vladykov (1949), Trautman (1957).

The most conclusive evidence that the smaller mature spring lampreys are freshwater parasitic *L. japonica* and not nonparasitic *L. lamottenii* was obtained by keeping immature adult specimens alive over winter in pens in Brooks Lake. In one experiment two immature adult lampreys caught in a fyke net in Brooks River in November 1962 were suspended six ft beneath the surface in a 100-ft^3 pen until mid-May 1963. The gonads and intestines of the lampreys could not be inspected because the specimens were to be kept alive. The dorsal fins were separate, no anal fin fold was evident, and the teeth were sharp and robust. In all external respects these two lampreys appeared identical with the many other immature adult *L. japonica* collected during the late summer and fall from throughout the system. When removed from the pen in May both lampreys, one male and one female, had almost fully matured and closely resembled the smaller mature lampreys commonly found in the spring.

Seasonal Distribution

Most streams in the Naknek system have the multiple gradient characteristics that Trautman (1957:133, 136) described as being suitable for lamprey spawning and ammocoetid growth and development. Many of the Naknek streams have not been surveyed for lampreys, but spawning or spent freshwater *L. japonica* have been collected from all major tributaries of Brooks Lake, from the principal lateral tributary of Lake Coville, from two lateral tributaries of Naknek Lake, and from Coville, Grosvenor, Brooks, and Naknek rivers (Fig. 1). The latest seasonal collection date of these lampreys was 19 July 1958, when a spent male was caught in a fyke net in Brooks River.

No spawning anadromous *L. japonica* have been observed in the Naknek system, although it is assumed that spawning occurs in the larger streams, probably in May and June. Six spent males and one spent and one ripe female were caught in fyke nets in Naknek River between 1 June and 16 June in 1961 and 1963. One spent male from the mouth of Brooks River was caught on 13 June 1963.

The immature adult lampreys are found primarily in limnetic areas of lakes and in interconnecting rivers between lakes in late summer and fall. A few recently transformed immature adults, however, have been caught in streams in June. These were taken from Naknek River, Grosvenor River, and the principal lateral tributary of Coville Lake. Forty-one immature adult *L. japonica* were captured in limnetic areas of lakes with tow nets in 1961, and 36 were caught in 1962 (Table 2). Limnetic lake samples of immature *L. japonica* were taken in every lake or major basin in which towing was conducted, except for the east portion of North Arm and the extreme lower end of Naknek Lake (Fig. 1). Brooks Lake produced the greatest numbers of open-lake samples in both 1961 and 1962. Immature adults taken in limnetic samples may represent transformed lampreys-of-the-year. The catch per unit effort in tow nets generally increased during the season, suggesting greater availability and possibly continuous recruitment into the lakes throughout the summer.

An apparent downstream migration of immature adult *L. japonica* from Brooks, Coville, and Grosvenor lakes begins in August and continues into the fall. At Brooks Lake, where collection data are most complete, they have been caught with fyke nets in Brooks River as late as mid-November. Collections of *L. japonica* migrating from Lake Coville and Grosvenor Lake were made in Coville and Grosvenor rivers in August in 1961 and 1962. No collecting in either of these streams was attempted later than early September. No fall or winter collecting has been attempted in Naknek River, and it is not known how many, if any, of these lampreys migrate through Naknek Lake into salt water.

A comparison of immature adults from areas of Brooks Lake and downstream migrants from Brooks River indicates that the larger individuals are leaving the lake. Thirteen *L. japonica* caught in tow nets in Brooks Lake between 27 August and 5 September 1962 averaged 159 mm in total length, while 15 specimens caught in fyke nets in Brooks River between 22 August and 25 September 1962 averaged 165 mm. Sixteen caught in fyke nets in Brooks River between 30 August and 3 September 1958 averaged 183 mm.

It is not known how many of the lampreys in the lakes take part in this late summer and fall migration, nor is the significance of the migration understood. If, as I suspect, the lampreys represent the freshwater form, the migration may indicate they have modified their original anadromous behavior and now feed and mature in downstream Naknek Lake before returning to streams in the upper lakes to spawn.

Although ammocoetes have been caught moving downstream into the lakes during spring, summer, and fall months, they are particularly evident in the spring. Length frequencies of ammocoetes migrating from Hidden Creek into Brooks Lake in the spring of 1963 (Fig. 2) indicate that more than one age-group is represented. This downstream movement of ammocoetes suggests that in many cases final transformation into adults may occur off the stream mouth or elsewhere in the lake. Many of the ammocoetes were partly transformed at the time of capture.

One partly transformed ammocoete caught in a fyke net in Brooks River in early June 1963 was maintained in a small aquarium until 31 May 1964. It had completely transformed by August, and although it had no opportunity to feed for nine months of adult life, it still maintained all the characteristics of a recently transformed parasitic lamprey. The teeth were sharp and robust and the intestine, although empty, was almost three mm in diameter. The gonads were poorly developed and the proportional body morphometry, particularly the eye size, resembled that of an immature adult parasitic lamprey.

Spawning Behavior

Periodic field observations on the spawning behavior of the dwarfed freshwater *L. japonica* were made on tributaries of Brooks Lake and in Brooks River between 1958 and 1962. The spawning behavior of this lamprey was quite similar to that recorded for other small lampreys: *Ichthyomyzon gagei* Hubbs and Trautman by Dendy and Scott (1953), *Lampetra aepyptera* (Abbott) by Seversmith (1953), and particularly *L. lamottenii* (= *L. wilderi*, see Hubbs, 1925) from eastern North America by Gage (1893, 1928), Dean and Sumner (1897), Young and Cole (1900), and others.

Nesting sites, which were observed in streams ranging from five to more than 100 ft wide, were all located out of the main current in water from three to eight inches deep and flowing from 0.5 to one ft/sec. Gravel usually varied from 0.5 to two inches in diameter. Spawning was always confined to a specific nest site from six to 10 inches in diameter that varied from a two- to three-inch well-defined depression to a shallow irregularity in the stream bottom. Water temperatures varied from 54° to 59° F. The earliest observed spawning was on 28 May, the latest on 2 July.

Table 2. Numbers of Immature Adult *Lampetra japonica* Caught in 10-ft Diameter Tow Nets in Naknek River System, 1961–1962. A standard tow was 1,500 ft long with the top of the net either on, or 10 ft beneath, the surface. Numbers in parentheses represent numbers of standard tows.

Lake or Basin	1961			1962		
	July	Aug.	Sept.	July	Aug.	Sept.
Lake Coville	0	8	3	0	1	
	(19)	(38)	(6)	(16)	(21)	
Grosvenor Lake	0	3	0	0	0	
	(31)	(77)	(2)	(32)	(25)	
Iliuk Arm	1	4		1	4	
	(20)	(29)		(36)	(36)	
South Bay	0	4	0	6	1	
	(33)	(20)	(4)	(41)	(20)	
North Arm		0		0	1	
		(32)		(47)	(48)	
Lower Naknek Lake		0		1	3	
		(22)		(28)	(28)	
Brooks Lake		10	8	0	12	6
		(59)	(99)	(83)	(56)	(12)

The number of spawners per nest site varied from two to eight and was usually five or six. There were usually fewer females per nest than males, and both sexes participated in the nest building. In perhaps the most common spawning activity, a lamprey would attach its oral disk to one of the larger stones in the nest area and then arch its body from this anchor point and thrash violently in the gravel with the posterior one-third of its body, raising small stones and silt which the current carried downstream. The spawners also picked up small stones with the oral sucker, and with the aid of the current carried the stones out of the spawning area. On one occasion a lamprey was observed to pick up a small sculpin (*Cottus* spp.) and carry it downstream from the nest. Sculpins were frequently seen around and in the lamprey nests and possibly fed upon lamprey

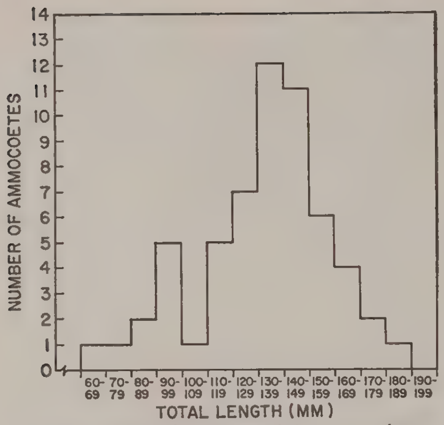

Fig. 2. Length frequency of *Lampetra japonica* ammocoetes caught in fyke nets from 24 April to 4 June 1963 in Hidden Creek, a tributary of Brooks Lake.

eggs. No defensive significance on the part of the lamprey is attached to the above incident. Dendy and Scott (1953) reported that minnows apparently fed on eggs of spawning *I. gagei.*

In the spawning act the male attached his oral sucker to the anteriormost dorsal portion of the female's head. Next the female arched her body upward and laterally toward the male. The male, also in an arched position, fixed the posterior portion of his body over the posterior of the female. When this embrace was complete the posterior one-third of the male was wrapped completely around the female so that the genital papilla of the male was close to the genital pore of the female. A rapid vibration by both individuals culminated the spawning act.

Apparently no monogamy in pairing existed among spawners. No aggressive behavior among males was observed, and a female that could be recognized by a scar appeared to spawn separately with three different males. This differs from the monogamous tendencies of *Petromyzon marinus* in Michigan (Applegate, 1950) but is similar to behavior noted for *I. gagei* by Dendy and Scott (1953) and for *L. lamottenii* by Dean and Sumner (1897). A spawning embrace where two males simultaneously attached to a single female was observed in One Shot Creek, a tributary of Brooks Lake, by Roger Trautman, a seasonal fishery aid. Dendy and Scott (1953) reported a similar incident while observing the spawning of *I. gagei* in aquaria.

Parasitism

An adult salmon counting weir is located on Brooks River at the outlet of Brooks Lake. Frequently in July and August a school of several thousand adult sockeye salmon group above this weir after passing upstream through the weir into Brooks Lake. On several occasions, particularly in 1958 and 1962, immature adult *L. japonica* were observed attached to adult sockeye salmon and rainbow trout, *Salmo gairdnerii* Richardson, in front of Brooks weir. These lampreys had probably started to migrate from the lake, and upon finding a large concentration of fish at the lake outlet, remained for additional feedings.

A 137-mm *L. japonica* attached to a 65-mm pygmy whitefish, *Prosopium coulterii* (Eigenmann and Eigenmann), was caught in a tow net haul in Brooks Lake on 22 August 1961. While skin diving in Brooks Lake on 12 August 1962, I caught a 148-mm *L. japonica* that was attached to a three-spined stickleback, *Gasterosteus aculeatus* Linnaeus, estimated to be 60 mm long. Scars, presumably from attacks by *L. japonica,* have been observed on lake-residing juvenile sockeye salmon and seaward-migrating smolts. *Lampetra japonica* undoubtedly parasitizes many of the other fishes present. No known freshwater lamprey parasitism, however, represents a detriment to any fish population in the Naknek system.

Adult sockeye salmon in the Naknek system frequently bear scars from lamprey attacks at sea. These scars are sometimes as large as 20 mm in diameter and could be made by large immature anadromous *L. japonica.* Birman (1950) attributed lamprey predation on pink salmon, *Oncorhynchus gorbuscha* (Walbaum), and chum salmon, *O. keta* (Walbaum), returning to the Amur River to ocean-dwelling *L. japonica.* Because Bristol Bay salmon stocks are known to range in the North Pacific far south of the Aleutian Island chain, some scars on adult Naknek sockeye salmon could also be made by ocean-feeding *L. tridentata* that do not follow the salmon past the lamprey's apparent northern range limit.

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Behavior of Displaced Adult Pink Salmon

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ABSTRACT

Studies to show whether pink salmon (*Oncorhynchus gorbuscha*, Walbaum) will repeat their original choice of spawning area when captured and transported to another location were done in Olsen Creek, Prince William Sound, Alaska, in 1961, 1962, and 1963. Fish to be displaced were anesthetized with MS-222 (except in 1961 when no anesthesia was used) and marked with Petersen disk tags. Equal numbers of control fish were treated in an identical manner and left at the donor site.

In 1961, 100 pink salmon were displaced from Olsen Creek beyond the entrance of the bay, a distance of more than 3 miles from the creek mouth. Of the 54 fish accounted for, 91% returned to Olsen Creek.

In 1962 and 1963, the displacements were confined to Olsen Bay. Fish displaced "on-route" achieved a higher rate of return than fish displaced "off-route." Further, under conditions of extremely low stream flow, displaced fish did not return to their original choice of spawning area. When stream flows were normal or high, they showed a strong tendency to return to areas of their original choice.

INTRODUCTION

Pritchard (1939) and Davidson (1934) in marking experiments demonstrated conclusively that pink salmon (*Oncorhynchus gorbuscha*, Walbaum) mature at 2 years of age and that they tend to return to their natal spawning gravels. Pritchard stated that isolated individuals, not economically significant, may wander up to 400 miles from the parent stream. Davidson felt that the precision with which pink salmon return to their home streams might depend on the proximity of other pink salmon streams. The degree, if any, to which pink salmon return to specific spawning areas within the same watershed is not known. Recent evidence by Hartman and Raleigh (1964) strongly suggests that sockeye salmon (*Oncorhynchus nerka*, Walbaum) were homing to specific tributaries in one small lake system.

Semko (1954) captured adult pink salmon in Karymaisky Spring, Kamchatka, and transported them in a floating trap downstream where they were tagged and released. Based on the small returns to Karymaisky Spring (21 of 151 fish released), Semko concluded that pink salmon lacked a strict attachment to specific spawning grounds.

Pink salmon spawn in the two forks of Olsen Creek in Prince William Sound, Alaska, and in the common intertidal stream channel. Obvious differences between the freshwater and intertidal environments and consistent differences in abundance and timing of pink salmon utilizing the two areas suggest that spawning could be linked to specific stream environments (Helle, Williamson, and Bailey, 1964).

During 1961, 1962, and 1963 the U. S. Bureau of Commercial Fisheries carried out a series of experiments at Olsen Creek designed to show if adult pink salmon, when displaced, would return to their original choice of spawning area. The objective during the first year was to determine if pink salmon spawners from Olsen Creek would return when transported back to salt water beyond Olsen Bay. The objective in 1962 and 1963 was to establish the degree of attachment of adult pink salmon to specific spawning areas within the Olsen Creek drainage. Knowledge of precision of homing is necessary to achieve optimum production by formulation of fishing regulations which will result in proper spawning escapements at specific times and in specific areas.

DESCRIPTION OF STUDY AREA

Olsen Creek is located at the head of Olsen Bay, in Port Gravina, Prince William Sound, Alaska (Figure 1). A physical and ecological description of the area is given by Helle et al. (1964).

The main stream is formed by the convergence at the 11-foot tide mark of two streams, East Fork and West Fork (Figure 2). Each

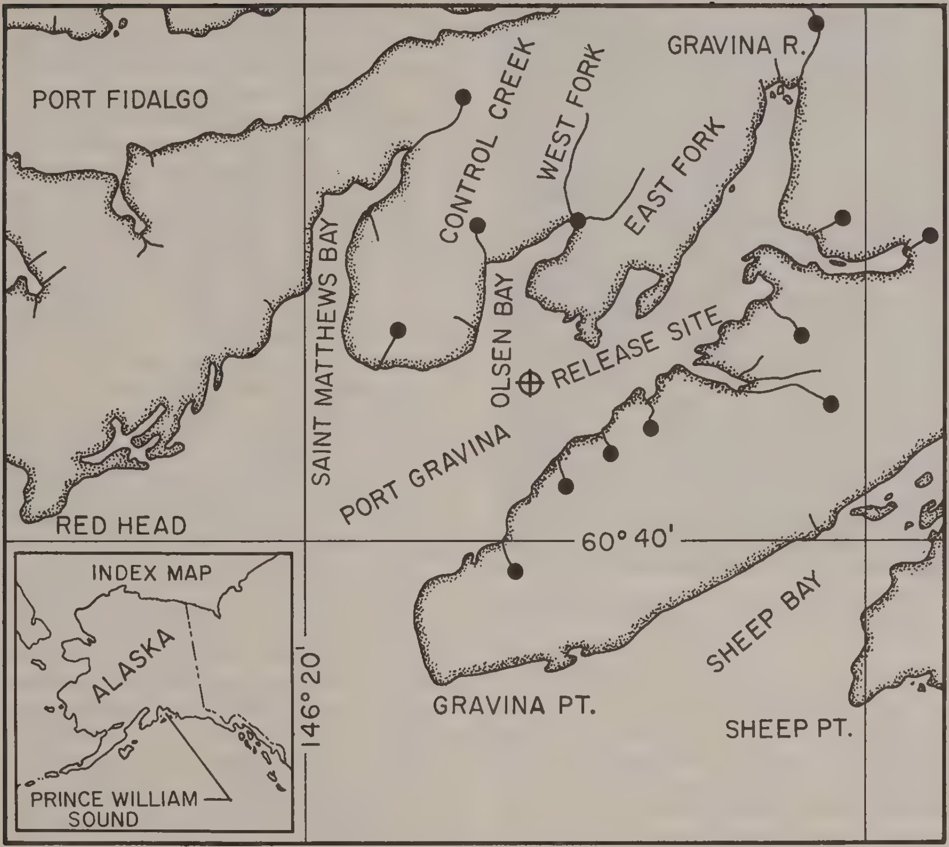
PORT FIDALGO
CONTROL CREEK
WEST FORK
GRAVINA R.
EAST FORK
SAINT MATTHEWS BAY
OLSEN BAY
RELEASE SITE
PORT GRAVINA
RED HEAD
60° 40'
INDEX MAP
ALASKA
PRINCE WILLIAM SOUND
146° 20'
GRAVINA PT.
SHEEP BAY
SHEEP PT.

FIGURE 1.—Port Gravina, Prince William Sound, where experiments on displaced adult pink salmon were conducted, 1961–63. The black dots mark Olsen Creek, the main study stream, and 12 small streams that were surveyed weekly for occurrence of tagged fish.

fork has an average summer discharge of about 33 cubic feet per second and an average width of 25 feet. Annual precipitation is about 100 inches and freshets of more than 100 cubic feet per second in each fork occur frequently (Helle et al., 1964). Average width of the main stream is about 70 feet. Both forks are accessible to pink salmon spawners for about 1.5 miles. The 12-foot tide mark (approximately mean high tide) is considered the separation point between the intertidal and freshwater stream areas. Although less than one-third of the total spawning area available is intertidal, about 75% of the total run of pink salmon spawns between the 4- and 12-foot tide marks.

Another spawning stream, Control Creek, is located on the north shore of Olsen Bay (Figure 1). This stream is smaller than Olsen Creek and has a falls preventing upstream salmon migration less than 200 yards upstream from the 12-foot tide mark. Actually, almost all of the accessible spawning area is subject to tidal influences.

Except for Gravina River the other spawning streams shown in Figure 1 are comparable in size and discharge to one of the forks of Olsen Creek. Gravina River is the largest watershed in Port Gravina, but it is not an important pink salmon producer. The size of spawning populations of pink salmon in Olsen Creek is usually 3 to 4 times greater than the

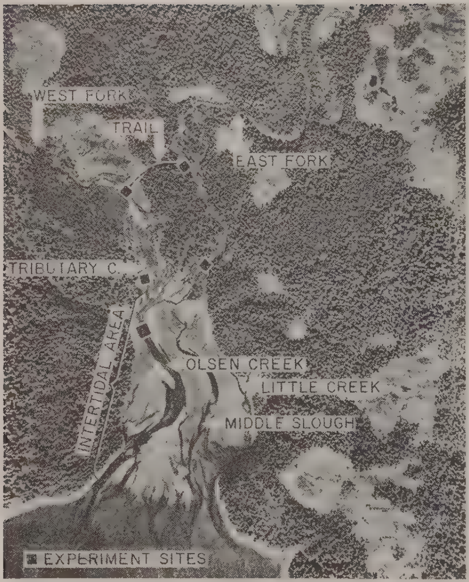

FIGURE 2.—Aerial view of Olsen Creek drainage and location of displacement experiment sites.

population in any of the other streams in Port Gravina. In 1961 and 1962 over 130,000 pink salmon spawned in Olsen Creek. The magnitude of the 1963 run was about half that of the previous 2 years. The timing of the spawning migration is similar in all the streams in Port Gravina.

EXPERIMENTAL PROCEDURES

In 1961 five male and five female pink salmon were captured at the 12-foot tide mark in the East Fork of Olsen Creek and placed in holding pens. They were tagged with Petersen disk tags and released at the capture site. These were termed nondisplaced fish. An equal number of pink salmon were captured in the same manner, tagged with different color combinations, placed in two tubs filled with water, and carried in a small boat to a release site about 3 miles from Olsen Creek (Figure 1). These were termed displaced fish. Time in transport was about 20 minutes. This procedure was repeated 10 times during the season (Table 1). Olsen Creek was surveyed daily for reappearance of the displaced fish, and 12 close salmon streams in Port Gravina were surveyed weekly.

In 1962 and 1963 pink salmon to be displaced were anesthetized with 0.25 g/gal MS-222 (tricaine methanesulfonate), tagged with Petersen disk tags, and placed in a wooden carrying box lined with ¼-inch neoprene and covered with wet burlap. Time in transport to the release site was recorded with a stop watch to the nearest minute. The displaced fish were put in a holding pen and released when they had recovered from the anesthesia. The stream was surveyed daily and locations of marked fish were recorded until they had definitely selected a spawning area. In most cases displaced fish were observed until they had spawned and died. Because in-stream tagging in 1960 and 1961 had shown no migration of Olsen Bay pink salmon to the east shore of Port Gravina (Helle et al., 1964), only the three pink salmon streams on the west shore of Port Gravina (Figure 1) were surveyed weekly in 1962 and 1963 for tagged fish.

Nondisplaced fish were anesthetized, tagged, and handled in the same manner as displaced fish including placement in the carrying box for the same amount of time as it took to transport the experimental fish, and placement in the recovery pen and release in the original capture area.

In 1962 and 1963 displacement experiments were confined to Olsen Bay mainly within Olsen Creek (Table 2). These experiments were of two types—"on-route" and "off-route." On-route experiments involved displacing fish downstream to learn if they would repeat their original choice of spawning area, while off-route experiments involved displacing fish to an area not traveled in their original migration.

Experiments 11 and 12 (Table 2) were off-route tests. Pink salmon were transported over a trail from the West Fork to the East Fork, so that they would have to drop back to the juncture in order to repeat their original choice of a spawning area. Another off-route test was tried in Experiments 15 and 17. Here pink salmon were displaced—a distance of more than 2 miles from the East Fork and Tributary Creek to Control Creek.

Experiments 13, 14, and 16 were on-route tests. Pink salmon were displaced from upstream areas to the intertidal zone to learn if

TABLE 1.—*Number and area of return of adult pink salmon displaced from East Fork of Olsen Creek, 1961*
[D denotes displaced; N, nondisplaced]

Experiment number	Date of release	Adult pink salmon released		Total accounted for		Adult pink salmon returned											
						Olsen Creek								Control Creek		Other creeks	
						East fork		West fork		Intertidal		Total					
		D	N	D	N	D	N	D	N	D	N	D	N	D	N	D	N
1	29 Jul	10	10	8	5	6	3	0	0	2	0	8	3	0	2	0	0
2	6 Aug	10	10	9	9	3	4	1	3	4	2	8	9	0	0	1	0
3	14 Aug	10	10	3	6	0	5	0	1	3	0	3	6	0	0	0	0
4	15 Aug	10	10	5	7	3	4	2	1	0	2	5	7	0	0	0	0
5	16 Aug	10	10	6	4	1	2	1	1	1	1	3	4	1	0	2	0
6	17 Aug	10	10	2	4	0	3	2	0	0	1	2	4	0	0	0	0
7	17 Aug	10	10	8	8	2	6	4	1	1	1	7	8	1	0	0	0
8	19 Aug	10	10	4	5	3	2	1	3	0	0	4	5	0	0	0	0
9	20 Aug	10	10	4	7	0	6	4	1	0	0	4	7	0	0	0	0
10	3 Sep	10	10	5	3	1	1	0	0	4	2	5	3	0	0	0	0
Total		100	100	54	58	19	36	15	11	15	9	49	56	2	2	3	0

they would repeat their original route at the stream juncture.

Experiments 18 and 19 were both of the on-route type, repeating Experiment 14 in 1962.

RESULTS

1961

Of the 100 tagged fish (50♂:50♀) displaced from Olsen Creek to Port Gravina, 54 were found later in spawning areas (Table 1). Because an equal number (27) of males and females were represented, the data were combined. Nine per cent of the fish were found in other streams, and 91% returned to Olsen Creek. In Olsen Bay 35% returned to the donor creek (East Fork), 28% to the West Fork, 28% to the intertidal area below the forks, and 4% to Control Creek.

Fifty-eight of the nondisplaced fish were found, and 62% of these remained at the donor site. Nineteen per cent dropped back to the juncture and chose the West Fork; 16% spawned in the intertidal area; and 3% migrated to Control Creek to spawn.

The final distribution of the displaced and nondisplaced fish showed a similar pattern (Figure 3). The fact that nondisplaced fish as well as displaced fish finally chose the West Fork, the intertidal zone, and even Control Creek, suggests that the pink salmon captured in the lower portion of the East Fork were a mixture of unsettled fish.

1962, 1963

Of the 91 tagged fish displaced in seven experiments in 1962, 65, or about 71%, were found later. Of these, 43% returned to the donor site (Table 2). Of the 49 fish displaced

TABLE 2.—*Displaced adult pink salmon returning to donor site and nondisplaced pink salmon remaining at donor site from experiments in Olsen Bay watershed, 1962 and 1963*
[D denotes displaced; N, nondisplaced]

Experiment number	Donor site	Release site	Date of release	Adult pink salmon released		Total accounted for		Displaced fish returning to donor site	Nondisplaced fish remaining at donor site
				D	N	D	N		
1962									
11	West Fork	East Fork	25 Jul	10	10	7	10	1	10
12	West Fork	East Fork	3 Aug	10	10	7	9	0	8
13	West Fork	Intertidal area	3 Aug	10	(1)	6	(1)	0	(1)
14	East Fork	Intertidal area	21 Aug	23	10	23	9	18	7
15	East Fork	Control Creek	21 Aug	10	(2)	6	(2)	1	(2)
16	Tributary C	Intertidal area	5 Sep	14	14	7	10	5	10
17	Tributary C	Control Creek	5 Sep	14	(3)	9	(3)	3	(3)
1963									
18	East Fork	Intertidal area	13 Aug	29	20	26	17	19	17
19	East Fork	Intertidal area	28 Aug	20	10	17	9	9	9

[1] Controls for Experiment 2 were considered controls for this experiment.
[2] Controls for Experiment 4 were considered controls for this experiment.
[3] Controls for Experiment 6 were considered controls for this experiment.

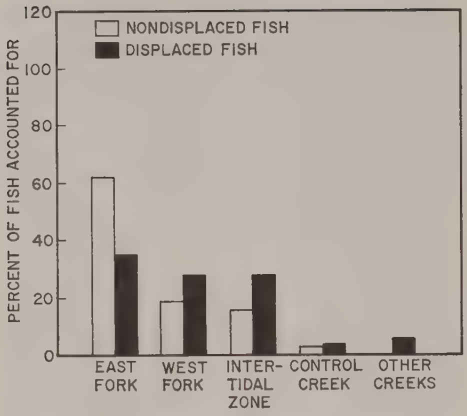

FIGURE 3.—Distribution of tagged pink salmon displaced from Olsen Creek, 1961.

in two experiments in 1963, 88% were found, and 65% of these returned to the donor site. Chi-square analysis showed that males and females in 1962 and 1963 returned with virtually the same frequency ($\chi^2 = 0.118$, 1 d.f.). The sexes were therefore combined in the data shown in Table 2.

Of the 20 pink salmon displaced off route and 10 displaced on route in the first three experiments in 1962, one returned to the original capture site. These experiments were performed between 25 July and 3 August, a period of unusually low rainfall and low stream levels (Figure 4). The first rainfall of any consequence occurred on 21 August and stream levels rose accordingly. Fish displaced on route from the East Fork to the intertidal area on this date showed a strong tendency to return to the original capture site (Table 2, Experiment 14): 18 of the 23 displaced fish returned. Two fish went up the West Fork and two dropped below the release site and spawned. One of the nondisplaced fish in this experiment dropped back to the juncture and went up the West Fork, and another spawned in Middle Slough. Ten fish were also displaced off route from the East Fork to Control Creek on 21 August. Although only one displaced fish actually returned to the donor site, three returned to Olsen Creek; two went up the West Fork and the other to the main stream intertidal area.

The last two experiments in 1962 were done on 5 September, when fish were displaced from Tributary C to the intertidal area and Control Creek. Only 7 of the 14 fish released on route in the intertidal area were found later on and 5 of these returned to the donor site. Nine of the 14 fish released off route at Control Creek were accounted for, and 3 of these returned to the donor site.

Stream level fluctuations were considered normal in 1963 (Figure 4), and returns from the two experiments (73% and 53%) were similar to returns from comparable on-route experiments in 1962 when water levels were also normal.

DISCUSSION

If all of the nondisplaced fish in Experiments 1–10 had remained in the East Fork, the final distribution pattern of the displaced fish would indicate that they preferred the Olsen Creek drainage and distributed themselves randomly in its three major spawning areas (Figure 3). Sixty-two per cent of the nondisplaced fish did remain in the East Fork but the other 38% spawned in the West Fork, the intertidal zone, and even in Control Creek. The similarity in final distribution between displaced and nondisplaced fish suggests something more selective than random distribution involved in occupation of particular spawning areas within the Olsen Creek Drainage.

The aim of the within-stream displacements in 1962 was to establish the degree of attachment of pink salmon for particular spawning areas. The unusual "drought" conditions provided an unexpected experimental situation.

The effect of the low stream levels in 1962 on the return of displaced fish can best be shown by looking at on-route (Figure 5) and off-route (Figure 6) experiments separately. Pink salmon displaced on-route displayed a much stronger tendency to return to donor sites than fish displaced off-route except for Experiment 13. This experiment was done during low water conditions.

The small return from fish displaced off route in Experiment 11 and 12 was probably the result of low stream levels. Off-route displacements to Control Creek made after stream levels had risen resulted in higher returns (Figure 6), even though they involved

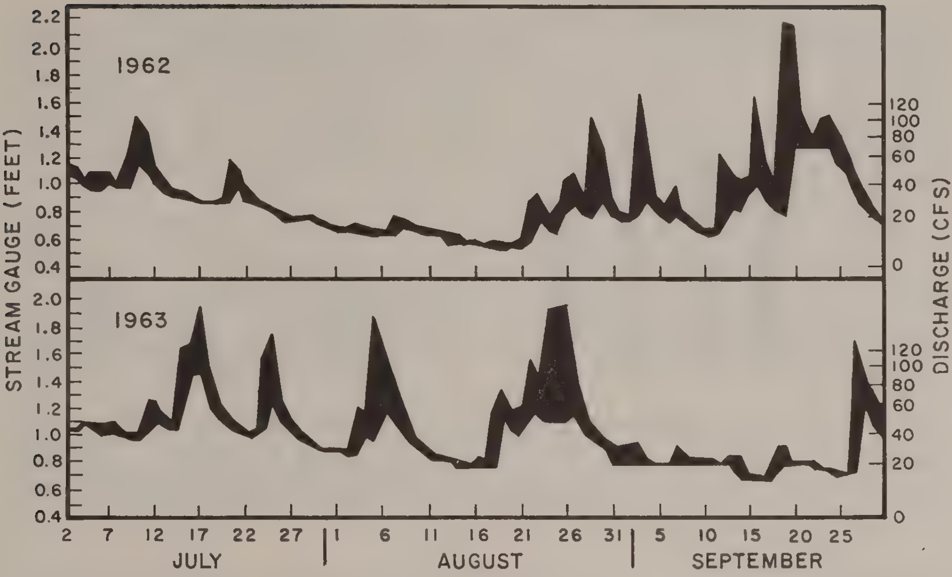

FIGURE 4.—Maximum and minimum stream level fluctuations in 1962 and 1963, East Fork of Olsen Creek.

a more complex problem in renavigation; and fewer returns might have been expected had water levels been the same.

Observations showed that movements of fish displaced during low water were impaired not only by reduced stream flow and depth but also by the confinement of other pink salmon spawners to a narrowed stream channel. In their efforts to move upstream or downstream, the displaced fish were chased and nipped continuously by fish of their own sex.

Displaced fish that repeat their choice at stream juncture or select a specific spawning area might not be homing to these areas but only displaying the ability to relocate a territory because of previous conditioning. This question was not directly resolved in the present study. Hartman and Raleigh (1964), however, demonstrated that sockeye salmon (*O. nerka*) at Brooks and Karluk Lakes, Alaska, show a definite tributary preference that is not the result of being conditioned to a stream prior to spawning but is a preference that exists in the adult sockeye before they even enter the lakes on their spawning migrations.

Sockeye salmon usually spend a year or more in freshwater after hatching while pink salmon migrate to the sea soon after emergence from the gravel. If adult salmon on their spawning migration identify their home streams through perception of some environmental characteristics imprinted during their natal freshwater existence as suggested by Hasler (1954), then it seems reasonable that the length of freshwater residence of the young would be related to the precision with which the adults returned to the natal areas. Sockeye salmon, because of a longer association with their natal freshwater areas, would be expected to be more precise than pink salmon in their homing ability.

Semko (1954) displaced salmon from Karymaisky Spring to the river below the mouth of the spring. Percentage returns for pink, chum (*O. keta*), and sockeye salmon were 13.9, 21.2, and 35.0, respectively. This order of return would be expected if the length of association with freshwater and estuary nursery areas by the young is proportional to the precision of return as adults to the natal stream. Compared with other studies, how-

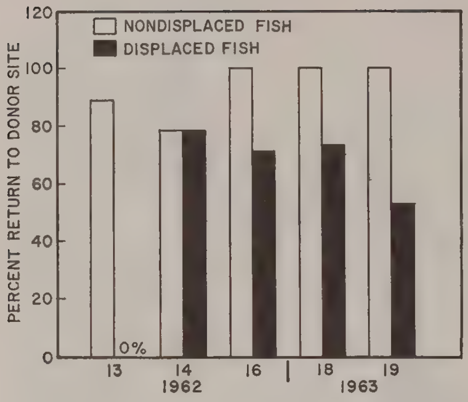

Figure 5.—Percentage of pink salmon displaced on route to the intertidal zone of Olsen Creek that returned to the donor site, and percentage of nondisplaced pink salmon that remained at donor site. (See Table 2 for location of donor sites.) Numbers at bottom of graph are experiment numbers.

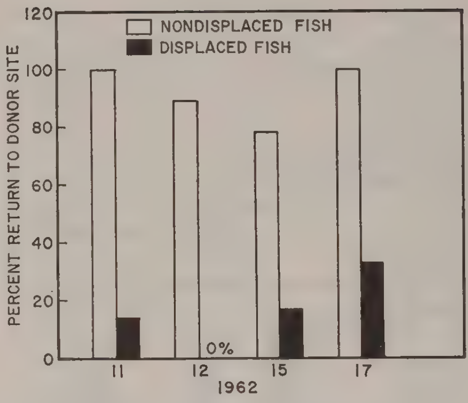

Figure 6.—Percentage of pink salmon displaced off route that returned to the donor site and nondisplaced pink salmon that remained at the donor site. (See Table 2 for location of donor sites.) Numbers at bottom of graph are experiment numbers.

ever, Semko's are low for sockeye salmon (Hartman and Raleigh, 1964) and for pink salmon (Pritchard, 1939).

Semko also transported spawners arriving at Karymaisky Spring back to the river above, below, and across from the mouth of the spring. The percentage of the total released that returned to the spring were 0, 9.6, and 8.7 for the respective experiments. Here, as well as in my study, pink salmon displaced off route did not return as frequently as those displaced on route. Semko could not account for about 84% of the 151 pink salmon displaced in 1944 nor for about 92% of the 147 displaced in 1945. He makes no statement about releasing nondisplaced fish as controls nor about searching areas other than the donor site for experimental fish, nor about the stage of maturity of the fish involved. Consequently, it is difficult to compare his work with other studies.

In Figures 3, 5, and 6, returns to the donor site are expressed as a percentage of the total accounted for rather than percentage of total released. This appears valid because surveys were for tagged fish, regardless of experimental origin. Every survey for experimental fish in Olsen Creek included a search of the entire watershed. For comparative purposes, the mean return of Experiments 14, 16, 18, and 19 (Table 2) was 69% of the total accounted for or 49% of the total released. These experiments were similar to some done by Semko (1954) in that fish were displaced on route. The mean value of 49% is considerably larger than the percentage return of any of the individual experiments done by Semko.

A factor that probably causes variation in returns of displacement studies is stage of maturity of the fish. All pink salmon examined were roughly at the same stage of maturation. The males had well-developed humped backs and elongated jaws, and both sexes were in full spawning coloration. These fish when displaced usually required about a week to spawn and die. Fish displaced late in the season (Experiments 16, 17, and 19), although they did not appear to be more advanced, spawned and died within 3 days after displacement. This shortening in stream life after displacement could be responsible for the reduced numbers of fish accounted for in the latter experiments. Helle et al. (1954) demonstrated a progressive seasonal reduction in stream life for pink salmon at Olsen Creek. This evidence suggests that displacement experiments of a complex nature should be done before the salmon are fully mature and about ready to spawn.

ACKNOWLEDGMENTS

Mr. John David Solf did the field work for the experiments in 1961. Messrs. Jack E. Bailey, Fredrik V. Thorsteinson and Richard S. Williamson of the U. S. Bureau of Commercial Fisheries participated in the planning and field work for the experiments in 1962 and 1963. Dr. Wilbur L. Hartman of the Bureau of Commercial Fisheries aided in preparing the manuscript.

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MAN IN THE SEA AND FISHERIES OF THE FUTURE

by

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Man in the Sea and Fisheries of the Future

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Abstract

The ability of man to live and work in the sea can lead to new or expanded utilization of bio-marine products. Production conceivably will pass through three evolutionary phases. The initial and today financially feasible phase will be the increased exploitation of high value resources: luxuries, delicacies, and pharmaceuticals adaptable to small scale harvesting operations requiring little or no culturing. Solution of legal problems and the discovery and growth of new markets including the support of new undersea establishments will lead to the second phase - the expansion of existing culture methods. Finally, the most promising future seems to lie in the establishment of large-scale farming operations in the sea. Vital to the success of these operations are undersea research facilities where studies in rearing, breeding, pest-control, in short all the processes that have made terrestrial agriculture what it is today, may be carried out with economically suitable marine organisms.

INTRODUCTION

There is little reason to doubt that the next few years will see man's occupation of the continental shelves. What will, in part, motivate this occupancy is the theme of this conference - Exploiting the Oceans. This extended capability to live and work in the sea will influence the exploitation of living marine resources. How this may happen is the theme of this paper.

Exploitation is an unfortunate word. Exploitation applied to fisheries implies the use of ocean resources with little regard to other than immediate monetary gain. With few exceptions this has been the historical fate of fisheries. Fortunately, there has been an increasing awareness that fishery resources are not limitless, and that the management and culture of marine organisms can have important economic advantages. These advantages will outweigh short-term profits taken without thought of continuing utilization. If, however, one is guided by the practices of the past it seems likely that the first commercial ventures to use man's extended submergence capabilities will be directed toward maximum profit in as short a time as possible. This type of venture is possible right now through the application of some of the new techniques to existing fisheries. These first commercial ventures will be followed in the next 5-10 years by attempts to increase and sustain production of certain marine resources through the application of culturing methods. These attempts to culture organisms in the deep sea will stimulate and in turn be aided by research made possible through the establishment of manned submarine laboratories. The knowledge gained from such underwater research centers would eventually have a profound effect on the fisheries of the future. Many of the problems that will influence this pattern of development are apparent today. Consideration of some of them will serve to point out the difficulties that face man-in-the-sea-type fishing operations.

FISHERIES OF THE IMMEDIATE FUTURE - LIMITED EXPLOITATION

In fisheries, diving has been a method used when no other method would do the job. Diving is not productive in terms of yield per man hour. It is uncomfortable, hazardous work and divers expect a high return for their effort. Because the method is not very productive the resource harvested must have a high value per unit. Diver produced products amount to only a minute fraction of the total yearly landings of fishery products. The output is aimed chiefly at the luxury market. There is little reason to suppose that the new advances in diving technology and physiology will change this emphasis from high-value, low-yield products to low-value, high-yield products. Instead, we may expect, in the near future, a continued production of the traditional items with perhaps an increase in some products that previously occurred at depths too great for full exploitation, and perhaps the exploitation of some new products which have recently been found to be of value.

The traditional diver-produced items have been shellfish, shell and pearls, sponges, coral, algae, and small quantities of fish and invertebrates for local or exotic markets. With few exceptions the annual production of these products has been on the decline. Changing tastes and lower cost synthetics have made most of these fisheries unprofitable. The extension of time and depth now possible through saturated diving and lock-out habitations and vehicles may revive a few of these fisheries.

The red and the black precious corals, when properly engraved, at one time were popular jewelry items. The sources of coral were chiefly the Mediterranean Sea and the seas of the Orient. These corals are deep-water species, the best growth occurring at depths in excess of 150 feet. Diving for coral in the past has been necessarily restricted and most harvesting was done by boats using drags and nets to break off and catch pieces of coral. Production was limited to a few thousands of pounds of coral a year worth $10 to $20 a pound. Although its popularity is not great, and the world market could easily be saturated, it does appear to be an item together with pearls, the other sea gem, that could be gathered profitably from small lock-out submersibles.

The same is true of sponges and some invertebrates that have apparent pharmaceutical value. Ectyonon from sponges, Holothurin from sea cucumbers, and Paolin II from some mollusks are promising drugs that will require a constant supply of raw material until they are synthesized.

Shell collectors pay well for rare specimens. The Glory-of-the-Sea cone, of which less than 2 dozen have been collected, sell for $500 and up each. Many of the rarer shells were dredged from deep water that is now accessible to divers. Once these and other shells are found in quantity and are no longer rare the price will drop rapidly, unless of course, conchologists increase in proportion to the world's population.

FISHERIES OF THE NEAR FUTURE

The above are some ways for man in the sea to make money fast from biological resources. All are possible today and require a minimum investment in both time and money. A larger investment in time and money is required to culture and harvest marine organisms. There have been several efforts to do this in the past, some have been highly successful such as the oyster and clam industries but these have not been true deep-sea farms. Others such as sponge farming, which in the Bahamas met with disaster in the form of a disease, have not been pursued in recent years.

There are a number of obstacles to cultivating marine organisms in commercial quantities. The most pressing is the legal question of establishing rights to a certain area of the continental shelf. Until this is decided there is little likelihood that any serious investments will be made in such ventures.

Even when the legal aspects have been solved the number of different organisms adaptable to culturing will be extremely limited for a number of years to come. Mariculture, the raising and harvesting of living marine products, to be economically successful requires the selection of a valuable product, knowledge of its growth needs, choice of a suitable locale, the ability to propagate the organism, the ability to control predation and disease, and the establishment of harvesting, processing and marketing facilities. These are all the problems faced by terrestrial agriculture transplanted to a difficult environment and complicated by a tremendous void in knowledge and practical experience. Taken in order the magnitude of these problems becomes apparent.

Selection of a Valuable Product

In this country, marine products are consumed as luxury items and gourmet foods, convenience foods, or used in manufacturing processes and agriculture. Marine products are not the chief source of our dietary protein nor are they likely to become so in the near future. With the exception of the luxury items chiefly shrimp, lobster, crabs, oysters, clams, scallops, other invertebrates, and a few fishes, the price to the producer, the fisherman, is very low. The harvesting of low-cost fishes covers vast areas of ocean and the yield in pounds per fisherman must be very high if a profit is to be made. The bulk of the catch is used for other than human consumption. The price to the fisherman for these fishes is on the order of 1¢ per pound. These species are not attractive subjects for mariculture. Of those species of fish used for human consumption a few bring more than 20¢ a pound and might be worth culturing. These values should be weighed against the price to the fisherman for invertebrates such as shrimp and lobster at better than 50¢ a pound.

Growth Needs

Most of the valuable marine organisms take several years to reach marketable size. The rate of growth depends to a great part on favorable oceanographic conditions that are poorly understood and even more difficult to control. The most valuable food fishes are carnivorous which means that their nutrient requirements will be a problem. Most of them are several links removed in the food chain from plants, the primary source of energy. Each link complicates and increases the cost of feeding the animal. Since these fishes are of a comparable monetary value with livestock and take longer to grow, it is difficult to imagine marine fish farming in the U. S. competing successfully with beef, pork, and poultry. However, the demand for sea food is increasing, partially as a result of successful promotion on the part of the industry, partially as a result of population growth. This increase in demand has resulted in an increase in value of some fishery products and may in time, coupled with a decrease in ocean fish stocks make fish farming more attractive.

Some fishes of potential value and many invertebrates are herbivores which should reduce the cost of production. Others feed on detritus or plankton which might be supplied through local enrichment of the water. These organisms which include abalone, sponges, the milkfish, some crabs, shrimp, bivalve mollusks, and some marine mammals, all have proved suitable subjects for cultivation.

Choice of Locale

All organisms have certain requirements for optimum growth. The choice of a site for an undersea establishment must consider the physical requirements of the animal with respect to temperature, salinity, available light which in some areas will limit the depth of the station, and a suitable surface or enclosure to contain the animals. A surface in the case of bottom dwelling forms may be artificially constructed or be an improvement of the natural bottom. In the case of organisms with high light requirements the surfaces might even be submerged rafts moored in deep water. Should the animal be an active swimmer, enclosures of some sort would be required. These might be fences or nets, curtains of air or perhaps electrical barriers. An intriguing possibility is the establishment of captive stocks in the hot water plumes offshore from proposed nuclear power plants. Cooling water from these plants may be expected to create pools of water several degrees warmer than the surrounding ocean. These pools might be stocked with tropical or semi-tropical species that could not cross the thermal boundaries of the pool.

Propagation

Many valuable marine animals undergo complicated and protracted larval development. The problems of rearing from egg to adult are great. Most successful culturing methods depend on natural growth through the larval stages, the organisms then being collected by providing a suitable bottom or surface on which the pre-adult can settle. The efficiency of this method could obviously be greatly increased were it possible to carry the larval stages through under controlled conditions or perhaps develop ways to shorten or eliminate some of the steps. This is an area in need of considerable research.

Predation and Disease

Predation losses in the sea may be expected to be highest during the early growth of the organism. Control of predators at this time in the life cycle will be very difficult unless hatching and rearing are carried out under artificial conditions. Once the organism has reached young adulthood the predators usually are sufficiently obvious that they can be controlled by physical or chemical means. (Grab the spear gun Henry the sheepshead is in the lobster hutch again.) Disease is a more serious problem. Some may be related to changes in the environment, others to cyclic changes in population densities, still others may be introduced through contamination. A disease can quickly wipe out a crop as has happened to the sponges in the Bahamas, oysters in numerous locations, the pearl oysters in the Gulf of California and other fisheries. Prevention and control of disease among marine organisms is still very poorly understood.

In the case of bottom dwelling forms this will probably be a job for divers or vehicles. Burrowing animals may be harvested electrically. Fishes may be rounded up using porpoise, men, nets, submarines, bubbles, electricity, even explosives. Processing the harvest may be done on the site and some of the by-products used for feed or fertilizer. It is doubtful whether it will be economical to establish sub-sea canneries and freezing plants, although this has been done for surface fisheries.

The sad state of fresh-fish markets in this country today is due in part to the lack of an assured supply of fish to meet fluctuating consumer demands. The establishment of stock-pens in the sea would allow orders to be filled on a day-to-day basis. Fresh fishery products might then become more prevalent in the large food-chain retail markets. The rapid turn over then possible would largely eliminate the many smelly, antiquated fish stores that have done little to help the popularity of sea foods in this country.

FISHERIES OF THE FUTURE

Mariculture depends ultimately on knowledge about the sea and its creatures. Most of this knowledge we do not have today nor are we likely to have it in the next few years. The greatest economic contribution that man in the sea can make to fisheries will be research. Scientific diving has been in existence for only a few years and its impact on biology has been remarkable.

The problems mentioned in connection with mariculture can be solved in the laboratory and field but the laboratory should be near the field - it should be in the sea. Laboratories on the continental shelves would be outstanding facilities for studying those problems that are difficult to simulate ashore. A laboratory complex extending from near-surface to depths of several hundred feet might be established either on a steeply sloping shore or as a series of tower complexes each with working surfaces and locks at various levels. A facility of this type would extend from the shelf up into the mixed layer and would simplify the study of a number of problems in marine biology. It would assure a continuous supply of sea water and nutrients and in situ conditions, so difficult to reproduce in shoreside laboratories, would prevail.

Those resources that apparently are not suitable for mariculture still may be assisted through the application of new knowledge gained by underwater observation and research. The improvement of fishing gear, in particular nets, has been aided in recent years by observation by divers, by manual sleds and submersibles, and at greater depths by cameras and television. Observations on the behavior of fishes at sea as opposed to their behavior in aquaria has been limited to date. In the future such observations should be possible for extended lengths of time and to much greater depths. Undoubtedly such observations will solve many perplexing problems that have limited the efficiency of some fisheries.

More important still, such observations may suggest ways to optimize the harvest of many marine resources. Aside from political considerations which often result in unrealistic measures, conservation of fishery resources tries to maximize the yield by controlling the size of the animal at capture and tries to limit the amount of the catch to a figure sustainable by the exploited population. The design of fishing gear that permits small fish or breeding stock to escape unharmed is a problem that may be solved through the study of fish behavior and fishing gear operation. Man's extended submarine capabilities make such observations feasible.

One of the most fascinating future possibilities is the use of marine animals as work animals. Training of porpoise and fishes may result in sub-sea "sheep-dogs" to tend fish schools and run errands. Some species of fish school with whales and porpoise. Recent successes with trained, free-swimming porpoise suggest that they might be used to lead schools of fish into nets or traps. Perhaps killer whales can be trained to ride herd on their commercially important cousins, the whale-bone whales. Here, incidentally, is a source of red meat from the sea that can be produced faster than the land can produce beef or pork. A blue whale doubles its birth weight in about a week, it grows from 2 to 20 tons in 6 months - about 200 pounds per day. Whales are a resource sadly in need of intelligent management today and perhaps some husbandry in the future.

The impact of man in the sea on fisheries will probably be slow, but eventually monumental. Diving technology has advanced much faster in this case than has fishery biology. The eventual economic contribution of man in the sea to fisheries may be far greater than the contribution of man in the sea to the exploitation of other marine resources. Fisheries, remember, can be renewable, inexhaustible resources if they are properly managed. This proper management can only come about through knowledge of the sea and its creatures. This knowledge can be gained by man in the sea.

Central Pacific Fishery Resources, State of Hawaii, Honolulu, 1966.

CATCHES OF BIGEYE AND YELLOWFIN TUNAS IN THE HAWAIIAN LONGLINE FISHERY

By

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ABSTRACT

Since its introduction in Hawaii in 1917, longline fishing has given rise to a fishery for yellowfin tuna (*Thunnus albacares*), bigeye tuna (*T. obesus*), and several species of billfishes. During 1949-64 the longline catch fluctuated between a low of 1.8 million pounds (990 metric tons) in 1963 and a high of 4.4 million pounds (2,420 metric tons) in 1953 and 1954. Landings vary seasonally. Bigeye tuna production reaches a peak in November or December and a secondary peak in March or April. Yellowfin tuna landings normally reach a maximum in June or July. Production of bigeye tuna has declined steadily since the record catch in 1953, whereas landings of yellowfin tuna have remained fairly stable. The decline in bigeye tuna production appears substantial, for catch per unit of effort has dropped to less than two-thirds of the 1956 level. On the other hand, catch rates for yellowfin tuna have increased about 3.5 times the 1956 level, and thus have approximately offset the reduction in number of fishing units in the fleet.

INTRODUCTION

A Japanese immigrant introduced longline fishing into Hawaii in 1917 (Otsu, 1954). Initial successes off Waianae, Oahu, caused the technique to be adopted in the offshore waters of the other islands. Today the longline fishery is a chief source of fresh fish for the Hawaiian Islands; it supplied from 1.8 to 4.4 million pounds annually from 1949 through 1964. The most important species caught are the yellowfin tuna (*Thunnus albacares*) and bigeye tuna (*Thunnus obesus*). Among the billfishes, the Pacific blue marlin (*Makaira nigricans*) and the striped marlin (*Tetrapturus audax*) predominate. Less important species are the broadbill swordfish (*Xiphias gladius*), sailfish (*Istiophorus orientalis*), shortbill spearfish (*Tetrapturus angustirostris*), black marlin (*Makaira indica*), wahoo (*Acanthocybium solandri*), albacore (*Thunnus alalunga*), skipjack tuna (*Katsuwonus pelamis*), and dolphin (*Coryphaena hippurus*). The tunas and most of the billfishes are consumed fresh, principally as "sashimi" (raw fish) and steaks. Some of the larger Pacific blue marlin, however, are frozen and used in the manufacture of "kamaboko" (fishcake).

LONGLINE VESSELS AND MODE OF OPERATIONS

The Hawaiian longline vessels are patterned on the Japanese sampan. They range from 28 to 62 feet in registered length, and weigh from 5 to 38 gross tons. They are powered with high-speed diesel engines of 115 to 165 horsepower. Although the longliners usually fish within 20 miles of shore, they are capable of wider operations; in recent years some have fished 300 to 400 miles from home port.

During 1949-52 the longline fleet consisted of 33 vessels based in Honolulu and 10 in Hilo (Otsu, 1954). The number of vessels remained nearly constant up to 1957, but has declined steadily since then. Between 1952 and 1964, 5 vessels shifted to other types of fishing, 3 were lost at sea, and 4 older vessels were withdrawn from the fleet, so that in 1964, 24 vessels were based in Honolulu and 7 in Hilo.

A fishing trip may last from 1 day to 15, depending on weather, fishing success, distance to fishing grounds, and such other factors as engine breakdown and loss or damage of fishing gear. Some of the smaller Honolulu vessels, which fish about 20 miles southwest of the city, make trips of 4-7 days; the larger vessels, which fish off the other islands, make trips of 8-14 days. A fishing trip averaged between 8 and 9 days during 1949-55 (Otsu, 1954 and Shomura, 1959). This average has remained almost constant.

Otsu (1954) reported that the vessels fished 20-35 baskets of five or six hooks each. Shomura (1959) reported that vessels less than 45 feet long fished an average of 26 baskets of five- to six-hook gear and larger vessels fished an average of 30-31 baskets of five- to six-hook gear. Although the small vessels still fish 20-30 baskets of five- to six-hook gear, some of the large vessels have increased their effort to 40-45 baskets of five- to eight-hook gear. One of the large vessels now regularly uses 60 baskets of five-hook gear; another vessel uses 80 baskets of four-hook gear. Most of the vessels operate with a crew of three or four fishermen, but some operate with as few as two and others with as many as five.

The lines are set out daily early in the morning and soaked until hauling begins late in the afternoon. Most vessels patrol their lines during the day to retrieve fish that have been caught. Depending on the success of the day's fishing, they either drift for the night or move to a new locality.

The vessels can carry from 3.0 to 7.5 tons of fish, but only rarely reach maximum capacity. Not equipped with mechanical refrigeration, they store the catch in fish holds with chipped ice. Prior to departure, the fish holds are packed with ice, usually in blocks, at a ratio of about 4 pounds of ice to every pound of anticipated catch (Otsu, 1954). The small vessels usually pack about 6 tons of ice and the large vessels about 16 tons. The ice is chipped as needed to store the daily catches.

The vessels usually carry several hundred pounds of bait on their fishing trips. Frozen sardines were formerly the principal bait species; because of the relatively high price of sardines, however, the fishery has turned in recent years to frozen saury (Cololabis saira).

HAWAIIAN LANDINGS, 1949-64

The annual Hawaiian longline catch during 1949-64 fluctuated between a low of 1.8 million pounds in 1963 and a high of 4.4 million pounds in 1953 and 1954 (fig. 1). The steadily decreasing landings of bigeye tuna were responsible for a decline from 1954 to 1964. The landings of yellowfin tuna have remained steady (fig. 1; see also table 1, Silliman, 1966). The yellowfin tuna was the dominant species in the longline catch prior to 1948 (Otsu, 1954), but since then the landings of bigeye tuna have surpassed those of yellowfin tuna. Before 1949, landings of bigeye tuna were small, usually less than 0.5 million pounds per annum. From 1949, the annual catch of bigeye tuna steadily increased to a high in 1953 of 2.8 million pounds, valued at $800,000. The landings later declined to a low of 0.8 million pounds, valued at $500,000, in 1964.

The percentage of bigeye tuna in the total Hawaii landings (all gear) from 1949 to 1964 fluctuated between 6.6 and 15.9 percent; that of the yellowfin tuna fluctuated between 1.8 and 5.5 percent. Although yellowfin and bigeye tunas constitute only a small percentage of the state's total commercial landings, they command relatively high prices, and thus contribute a large percentage to the value of the landings. The average annual price for the two species was about 30 cents per pound during 1950-56, but through 1964 the price of bigeye tuna tended to increase more than that of yellowfin tuna (fig. 2). The greatest price difference was in 1964, when bigeye tuna sold for an average of 59 cents per pound and yellowfin tuna for 37 cents per pound.

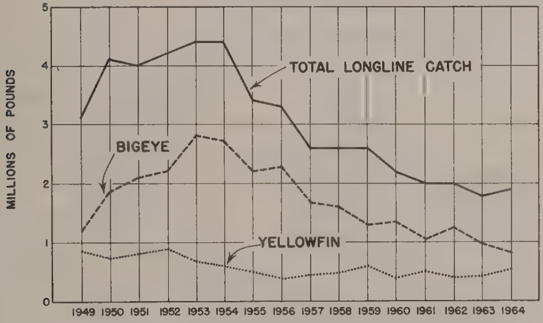


Figure 1.--The annual longline landings of bigeye tuna, yellowfin tuna, and total catch for Hawaii, 1949-64.

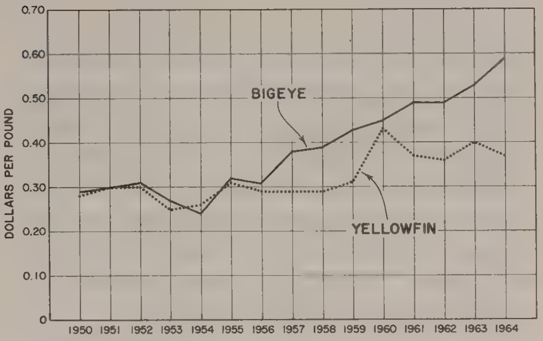


Figure 2.--Average annual auction prices per pound of bigeye and yellowfin tunas landed in Hawaii, 1950-64.

SIZE OF YELLOWFIN AND BIGEYE TUNAS

Longline gear selects relatively large fish (Murphy and Shomura, 1953). Yellowfin tuna landed in recent years have ranged from 11 to 270 pounds. Bigeye tuna have ranged from 20 to 300 pounds. The annual average weights of bigeye and yellowfin tunas landed in the Hawaiian longline fishery fluctuate between 135 and 170 pounds. Average weights of yellowfin tuna landed from 1949 to 1952 ranged from about 139 to 145 pounds, of bigeye tuna from 157 to 162 pounds (Otsu, 1954). The sizes of both bigeye and yellowfin tunas in the catches were larger in the summer than in other seasons (Shomura, 1954). Although Shomura found that the large vessels caught larger bigeye tuna than the small vessels, this difference was not noted in the yellowfin tuna.

SEASONAL VARIATIONS IN THE CATCH

Bigeye tuna occur in Hawaiian waters in greatest abundance from October through May (Otsu, 1954; Shomura, 1959).

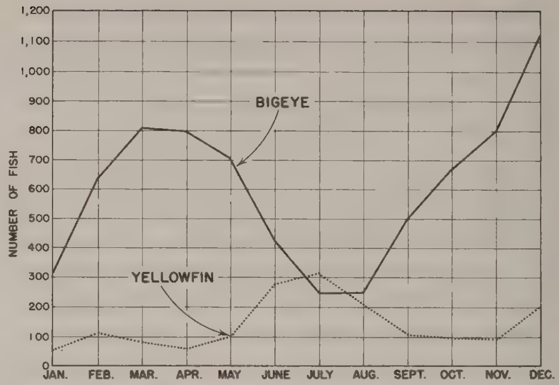
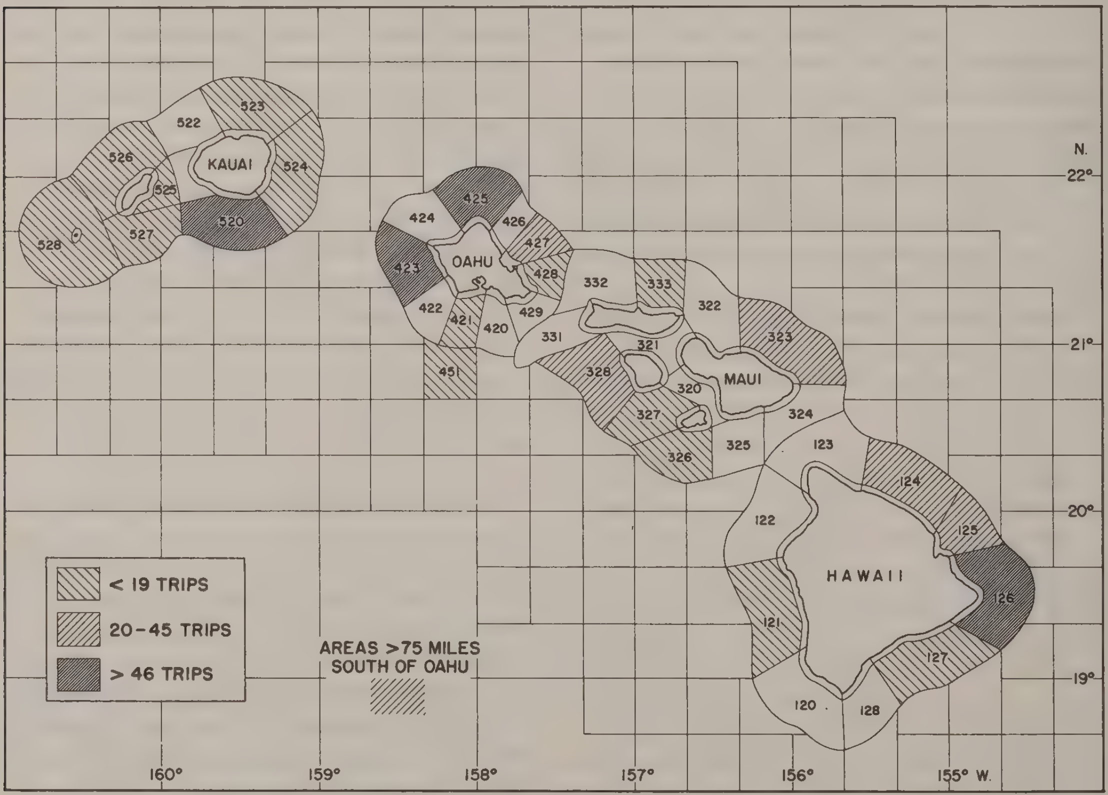


Figure 3.--Average monthly number of bigeye and yellowfin tunas landed in Hawaii, 1956-64.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157°
156°
155° W.
< 19 TRIPS
20-45 TRIPS
> 46 TRIPS
AREAS >75 MILES SOUTH OF OAHU

Figure 4.--Areas fished by Honolulu-based longline vessels in 1961. The area numbers were taken from the Hawaii Fish and Game Fisheries Chart No. 2.

Yellowfin tuna are most plentiful during the summer (fig. 3). The low average catch of bigeye tuna in January is primarily the result of shorter and fewer trips during the month, when the fleet remains in port about 10 days as part of an extended holiday. The high December catches are due mostly to the increase in the number of trips made by the vessels to take advantage of the strong demand for "sashimi," a traditional Japanese dish for the New Year holiday.

The longline vessels move throughout the islands in search of good fishing grounds. In winter most of the bigeye tuna are caught off the northern and northeastern coasts of the southern islands, Hawaii and Maui. Yellowfin tuna are fairly abundant off the southern and southwestern coasts of the northern islands, Kauai and Oahu, in the summer. Much effort is expended in those waters during the respective seasons. Figure 4 shows the statistical map used by the Hawaii Division of Fish and Game to designate areas where fish are caught. Indicated on the chart are areas where the Honolulu-based longliners operated in 1961. The numbers of trips made by these vessels in the statistical areas in 1961 are listed in table 1.

CATCH PER UNIT OF EFFORT

Studies of the relative abundance and availability of tunas in the fishery have defined catch per effort differently. Otsu (1954) used catch in numbers per 100 hooks as his index of relative abundance. Bigeye tuna catch rates attained by the Honolulu-based longline vessels increased from 1.08 per 100 hooks in 1949 to 1.80 in 1952. Catch rates of yellowfin tuna were fairly stable, varying from 0.33 to 0.43 per 100 hooks for the same years. After he found little vari-

Table 1.--Number of trips made into various statistical areas, as shown on figure 4, by Honolulu-based longliners in 1961

Statistical area	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
121	-	-	-	-	-	-	1	1	-	-	1	-
124	6	9	5	7	5	-	-	-	-	-	-	-
125	2	6	5	1	3	3	-	-	-	1	1	3
126	-	2	2	6	9	2	-	2	7	9	11	26
127	-	-	-	-	-	-	-	-	-	2	1	-
323	1	3	3	4	4	2	3	3	1	-	-	-
326	-	-	-	-	-	1	-	-	-	-	-	-
327	1	3	-	-	-	-	-	-	-	-	-	-
328	5	3	3	1	3	2	2	2	3	1	2	2
333	-	-	1	-	-	-	-	-	-	-	-	-
421	1	-	-	-	-	-	-	-	-	-	-	-
423	15	15	14	15	10	20	14	21	20	10	4	-
425	-	2	2	5	5	8	4	6	4	5	5	5
427	-	1	-	-	-	-	-	-	3	4	7	15
428	1	-	-	-	-	-	-	-	-	-	-	-
451	-	-	-	-	-	1	-	-	-	-	-	-
520	1	2	10	6	9	10	8	5	4	7	6	6
523	-	-	-	-	-	-	-	-	-	-	1	3
524	-	-	2	-	-	1	-	-	-	-	-	-
525	-	-	-	-	-	-	-	-	-	1	-	-
526	-	-	-	-	-	-	2	2	1	2	2	2
527	-	-	-	-	-	-	-	2	-	-	-	-
528	-	-	2	-	-	-	-	-	-	-	-	-
>75 miles south	-	-	-	-	2	2	7	4	1	2	2	-

ation in the number of units of gear fished per day by the vessels, Shomura (1959) used catch in numbers per trip in analyzing the catches of selected Honolulu-based vessels. Catch rates of bigeye tuna reported by small vessels were much lower than those of large vessels, but catch rates of yellowfin tuna were about the same for both sizes of vessels. By analysis of the catch by vessel size for 1948-55, Shomura showed that catch rates of bigeye tuna by large vessels increased steadily from about 7 fish per trip in 1948 to about 22 in 1953, and then declined slightly to 20 fish per trip in 1955. Catch rates of bigeye tuna for small vessels fluctuated between 3 and 10 fish per trip during the same period, and displayed no definite trend. The catch of yellowfin tuna for the same period showed a general decline from between four and five fish per trip in 1948 to about two fish per trip in 1955.

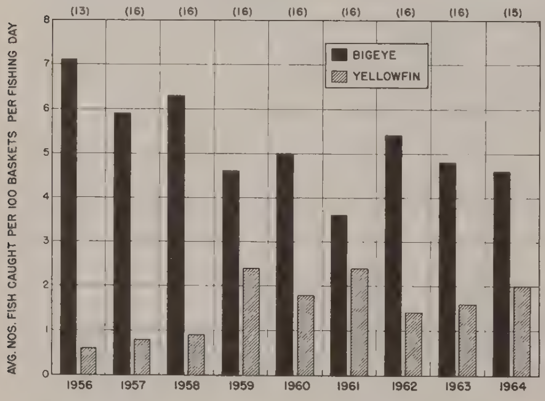

Figure 5.--Average annual catch rate of number of bigeye and yellowfin tunas per 100 baskets per fishing day of selected Honolulu-based vessels in all areas, 1956-64. The numbers of vessels contributing to the analysis appear in parentheses.

I have used catch in numbers per 100 baskets per fishing day as the measure of effort in analyzing the bigeye and yellowfin tuna catches from 1956 to 1964, because accurate hook data were not available to express the catch rates in numbers per 100 hooks. Catches of

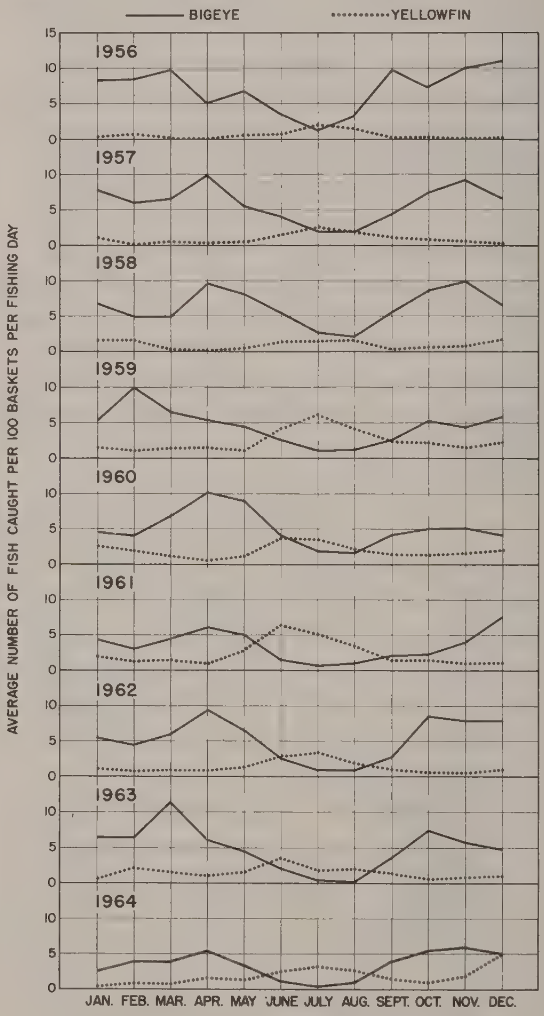

Figure 6.--The average monthly catch rates of bigeye and yellowfin tunas of selected Honolulu-based vessels fishing in the numbered statistical areas shown in figure 4, 1956-64.

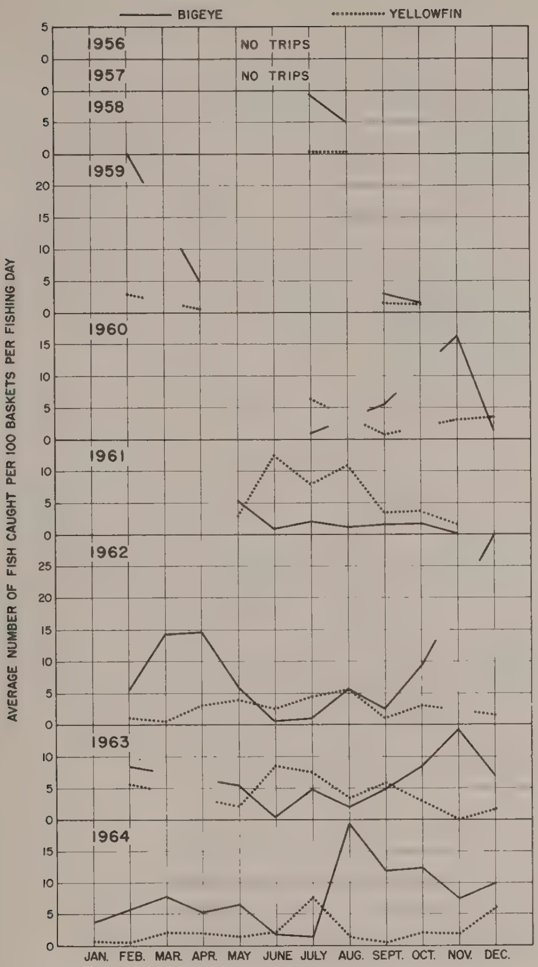

Figure 7.--The average catch rates of bigeye and yellowfin tunas made by selected Honolulu-based vessels fishing more than 75 miles south of the islands, 1956-64.

bigeye tuna generally declined from 7.1 fish per 100 baskets per fishing day in 1956 to 4.6 in 1964 (fig. 5). During the same years yellowfin tuna catches increased from 0.6 fish per 100 baskets per fishing day in 1956 to 2.0 in 1964 (fig. 5). The average monthly catch rates for the two species made in the numbered statistical areas shown on figure 4 from 1956 to 1964 are shown in figure 6.

I have analyzed catches of bigeye and yellowfin tunas by selected Honolulu-based vessels fishing 100 to 400 miles south of the island in 1956-64. Although trips into the southern area were too few to show annual trends, some of the best catch rates for bigeye and yellowfin tunas were attained there (fig. 7). The southern area was hardly fished by the longliners in the past, but the fishing success of a few vessels has induced a steadily increasing number of others to venture farther south of their regular fishing grounds.

ACKNOWLEDGMENTS

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RESULTS OF BOTTOM TRAWLING IN INDIAN SEAS BY R/V ANTON BRUUN IN 1963

by

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ABSTRACT

One hundred and four successful hauls were made by the Anton Bruun in the Bay of Bengal and in the Arabian Sea, utilizing a 13-m. Gulf of Mexico shrimp trawl.

The highest catch rates in the Bay of Bengal were obtained in depths of 15 - 37 m. in the Burma and East Pakistan regions. Stingrays, guitarfish and croakers were the most important organisms in the catches.

The highest catch rates obtained in Arabian Sea were in depths of 38 - 73 m. off the southeastern Arabian coast. The stingrays were the most important group in the catches. Other prominent groups in the catches were the swimming crabs, sciaenids, croakers, lizardfish, cardinal fish and threadfins.

A large part of the catches consisted of small fish weighing less than 250 g. each which was considered of very low market value.

The highest catch rates generally were obtained on Cruise 4B in areas of well mixed water.

INTRODUCTION

Exploratory bottom trawling surveys were carried out by the U.S. Bureau of Commercial Fisheries in the Bay of Bengal and in the Arabian Sea in 1963 as part of the field work of the U.S. Program in Biology. The program represents a major contribution of the United States to the International Indian Ocean Expediton (IIOE). This expedition, sponsored by UNESCO, is a multi-

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nation effort to delineate the topographic features, circulation and distribution of living organisms in the Indian Ocean and adjacent seas.

Bottom trawling was conducted from the R/V Anton Bruun, the former presidential yacht Williamsburg, which has been converted for oceanographic and biological research for the National Science Foundation. This twin screw vessel, which has 1100 SHP direct diesel drive on each shaft plus a 150 SHP active rudder, is 74 m long and weighs 1,421 metric tons (Fig. 1).

The major objectives of these surveys were: (1) to gain information on the distribution and relative abundance of fish and shellfish inhabiting the continental shelf and slope regions, and (2) to obtain specimens for systematic and other biological studies. These objectives were pursued in the hope that information gained would aid those countries bordering the Bay of Bengal and Arabian Sea to utilize the marine resources of these waters to a greater extent. The survey of the Bay of Bengal was carried out from March 12 to April 11, 1963, (Cruise 1) while that of the Arabian Sea took place from November 12 to December 10, 1963, (Cruise 4B).

HISTORICAL BACKGROUND

Surveys of the Bay of Bengal up to 1959 were mostly of the expeditionary type with little emphasis placed on commercial trawling aspects. In 1959, the Government of India started trawling surveys off the coast of Waltair as part of its third 5-year plan. These surveys were directed by a fisheries expert from FAO (Naumov, 1961, p. 60 and Borisov, 1962, p. 29), and the area covered was a narrow band along the northwestern part of the Bay of Bengal. The principal gear used was otter trawls. Explorations were conducted in waters ranging in depth from 12 to 160 m, with most of the trawling being done between 35 and 55 m. The largest catches generally were made in depths from about 40 to 60 m. Fishes frequently taken included sea catfishes (Arridae), lizardfishes (Synodontidae), croakers (Sciaenidae), goatfishes (Mullidae) and threadfin breams (Nemipteridae).

A Burma-Japan cooperative bottom trawling survey was conducted off Burma in the Gulf of Martaban in 1953-1955 (Ba Kyaw, 1956, p. 4). The largest catches were made where the water depth was about 54 m. The most common fishes in the catches were croakers, grunts (Pomadasyidae), snappers (Lutjanidae), leiognathids and lizardifishes. It was reported that from one-fourth to one-third of the catch was comprised of small fishes of no commercial importance.

In the Arabian Sea large scale trawling experiments were started in 1946 after the establishment of a pilot deep-sea fishing station in Bombay. During the period 1949-1955, intensive fishing with otter and bull trawls was conducted from shallow water to a depth of about 73 m (Jayaraman et al, 1959, p. 87). Largest catches were made in a depth of about 37 m and included perch, threadfins (Polynemidae), sea catfishes, eels and elasmobranchs.

Recently, two Soviet tropical class stern trawlers were reported to have carried out successful bottom trawling operations along the southeastern Arabian coast (Hinds, 1964, p. 3).

Most of the surveys off India and West Pakistan were conducted in depths less than 70 m. This was in line with the idea of providing immediate assistance to the existing fishery which is concentrated along a narrow coastal belt on the inner continental shelf. The Gulf of Kutch region was considered to be one of the richest grounds in the Arabian Sea (Seshappa, 1958, p. 14). The catches usually consisted of many species of fish, and only rarely were they dominated by one or two species. The best catches of shrimp were made in depths less than 22 m.

GEAR AND METHODS

The primary sampling gear was a nylon Gulf of Mexico shrimp trawl (Schaefers and Johnson, 1957, p. 17) measuring 13 m along the foot rope with a mesh size of 3.8 cm (stretched measurement, opening including 1 knot). A 46-m long bridle connected the trawl to a single towing warp. A rectangular otterboard measuring 0.8 x 1.5 m and weighing 73 kg was attached to each wing of the net when trawling to depths to 366 m. Below 366 m heavier boards (179 kg each) were used.

Echo soundings of the ocean bottom were taken whenever the Anton Bruun was under way. A general criterion was followed which required that approximately 5 km of relatively flat bottom was present before a trawl haul was attempted. Echo soundings were supplemented by samples of bottom sediments obtained with a small dredge or a spring-loaded bottom grab prior to trawling.

The trawl was towed from the starboard side off an A-frame and was set out at a vessel speed of about 6 to 8 knots with the cable being payed out at a rate of 40 to 60 m per min. The cable out-to-depth (scope) ratios were consistent with those found to be satisfactory in exploratory trawling with identical gear in the northeastern Pacific Ocean (Pereyra, 1963, p. 4). Ratios ranged from 6:1 in shallow water to about 3:1 in deep water. Except when snags or other hazards were encountered, the trawl fished for 30 to 45 min, (time trawl was on bottom) on Cruise 1 while on Cruise 4B the trawl fished for 45 min. in depths less than 183 m and for an hour at greater depths. Trawling speed ranged between 2 and 3 knots. Several features of the vessel which may have adversely affected the results were: (1) her relatively deep draft made it necessary to trawl only in depths greater than 15 m; (2) her propellers stirred up mud and sand in depths of about 22 m and shallower which may have frightened fish away from the path of the trawl, and (3) difficulty in maintaining proper trawling speed necessitated intermittent use of an active rudder in conjunction with the port engine which often resulted in a variable speed during the course of a trawl drag.

Following each haul, the cod end was lifted aboard the vessel by a small hydraulic crane and the catch was emptied onto a sorting table (Fig. 2) where it was separated by family (genera or species when possible). The total weight and number of individuals in each family of fish and each group of shellfish were recorded and representative samples of the catches were preserved. The preserved samples were shipped to the Smithsonian Institution in Washington, D.C. Other information obtained for most groups included length ranges and average weights. Length frequencies were taken from representative samples of some groups of fishes. For the larger shrimp catches, estimates of the number of whole shrimp per pound were recorded. Some of the specimens in good condition were photographed on a lightbox (Ronholt, 1963, p. 4) before being preserved.

TREATMENT OF DATA

In order to evaluate the catches in such a large survey area, it was decided to segregate the stations into several regions which generally were made to coincide with the geographic boundaries of the countries involved. The stations on Cruise 1 were divided into the Andaman Islands, Thailand, Burma and East Pakistan (Fig. 3); while regions used for Cruise 4B were India, West Pakistan, Gulf of Oman and Arabia (Fig. 4). Stations in each region then were grouped according to depth ranges of 15-37, 38-73, 74-110, 111-183, 184-366 and 367-549 m. The depth of each haul was determined as the average of the starting and ending depths.

Relative abundance of the fish and shellfish encountered was examined by comparing their catch rates in kilograms caught per hour of trawling. Average catches in kilograms per hour of trawling were computed by dividing the sum of the catches by the total effort for individual depth intervals within regions. Catch rates were computed for elasmobranchs, flatfish, eels, roundfish, squid and crustaceans but were not calculated for snakes, corals, echinoderm, crincids, gastropods, coelenterates, tunicates and sponges since the latter were not believed to be quantitatively sampled by the trawl.

RESULTS

Bay of Bengal

Between March 12 to April 11, 1963 trawling on Cruise 1 was conducted east of the Nicobar Islands to the west coast of Thailand, off the southern and western coasts of Burma, along the eastern coast of the Andaman Islands and along the coast of East Pakistan. Although sampling was conducted within the general depth range of 15 to 516 m, most of the trawling occurred on the continental shelf (to depths of 183 m). The continental shelf was usually trawlable but there were occasional outcroppings of coral and rocky bottom which prevented trawling. The continental slope at depths from 183 to about 900 m was usually too precipitous for effective trawling. The bottom at depths greater than about 990 m was usually flat and muddy and suitable for trawling.

Bottom sediments varied considerably between regions. Off Burma they consisted of grey mud with some sand and combinations of mud, sand, shell, shale and coral. Sediments off East Pakistan were mostly greenish-grey mud with some sand. Greenish mud with combinations of sand, shell, hard clay and rock predominated along the eastern coast of the Anadaman Islands. Off Thailand, sediments were mostly greenish clay, shell, mud and coral.

Thirty-one trawl hauls were made in the Bay of Bengal, of which 27 were successful and 4 resulted in extensive damage or loss of the nets. The highest incidence of gear damage occurred off Thailand where there were numerous outcroppings of coral. Largest catches were obtained off Burma and East Pakistan (Fig. 5). Catch rates of fishes and invertebrates for the different regions are shown in Table I through IV.

Andaman Islands

A haul taken in the 38-73 m depth range and two hauls made in the 74-110 m depth range resulted in relatively small catches ranging from 0.5 to 23 kg per hour of trawling. The catches were comprised of 2 families of elasmobranchs, 2 families of flatfish, 16 families of roundfish, and a few squid. Aside from a 23 kg stingray (Dasyatidae), which was caught in the 74-110 m depth range, the catches were negligible. No shrimp or eels were caught in this region.

Thailand

Single hauls taken in the 38-73, 74-110 and 367-549 m depth ranges resulted in relatively poor catches ranging from 1 to 19 kg per hour of trawling. Represented in the catches were 3 families of flatfish, 1 family of elasmobranchs, 2 families of eels, 29 families of roundfish, shrimp, crabs, octopods and cuttlefish. The highest catch rate occurred in the 38-73 m depth range where lizardfishes were the most important group taken.

East Pakistan

Six hauls made in the 15-37 m depth range resulted in catch rates ranging from 11-148 kg per hour of trawling. Five families of elasmobranchs, 2 families of flatfish, 33 families of roundfish, shrimp, crabs, scyllarids, sepiolids and loliginids were present in the catches. The fact that the guitarfishes

(Rhinobatidae) yielded the highest catch rate (27 kg per hour of trawling) was due entirely to the capture of one large individual. Other important fishes in this depth interval were croakers, sea catfishes and threadfins. The average catch of shrimp amounted only to 2 kg per hour of trawling.

Burma

Catches off Burma consisted of 3 families of elasmobranchs, 5 families of flatfish, 57 families of roundfish, eels and 9 groups of invertebrates. Highest catch rates were obtained in the 15-37 m depth range followed by those in the 184-366, 367-549, 38-73 and 74-110 m depth ranges, respectively. Stingrays and croakers were the most prevalent fishes caught in the 15-37 and 38-73 m ranges. Snappers were the most important group in the 74-116 m depth range. The catch in the 367-549 m depth range consisted mainly of an unidentified berycoid fish and shrimp. Only small quantities of shrimp were caught in the shallower depths and the fair quantities of those found in the deeper waters were not the usual commercial species.

Other factors besides the generally small fish catches suggested the ocean floor in the regions surveyed in the Bay of Bengal was rather barren of life. Very few sea stars were encountered anywhere. Many shells of mollusks and other invertebrates were brought up in the trawl, but almost all of them were empty.

Arabian Sea

The survey on Cruise 4B was made from November 12 - December 10, 1963, starting from Angria Bank, off Bombay, then proceeding along the continental shelf into the Gulf of Oman and terminating off the eastern coast of Arabia (South of Al Masirah). The depths trawled ranged from 16-366 m. No trawlable grounds were found in the vicinity of Angria Bank where the bottom was mostly of coral. The area between Bombay and Karachi offered the largest trawling grounds with its wide shelf characterized by extensive flat muddy bottom. The continental shelf from Karachi to the Gulf of Oman was relatively narrow compared to that east of Karachi. The Gulf of Oman contained fairly extensive grounds but there were occasions where coral and great quantities of dead shells hampered trawling. Hard and irregular bottom prevailed off the Arabian coast.

Of the 86 trawl hauls made, 77 were accepted as satisfactory for use in the catch analysis. The total trawling time of 60 hours was broken down as follows: 21.3 hours off India; 22.0 hours off West Pakistan; 15.4 hours in the Gulf of Oman; and 1.3 hours off Arabia. Average catches in kilograms per hour of trawling for each organism caught in the Arabian Sea are shown by depth ranges and regions in tables V through VIII. Highest catch rates were obtained off the Arabian coast, followed by those off Indian and West Pakistan (Fig. 6).

India

Twenty-eight hauls in this region resulted in catches ranging from about 1 to 439 kg per hour of trawling. Represented in the catches were 4 families of elasmobranchs, 4 families of flatfish, 4 families of eels, 48 families of roundfish, and 8 groups of invertebrates. The most productive depth range surveyed was from 15-37 m, followed by those from 111-183, 74-110, 38-73, 184-366 m, respectively. Threadfin breams provided the highest catch rates in this region, dominating catches in the 111-183 and 74-110 m depth ranges. Stingrays were the next most important group and dominated catches from the 15-37 and 38-73 m depth ranges. Other important fishes caught were croakers, threadfins, and lizardfishes. The small shrimp catches were mostly from the shallower depths.

West Pakistan

Twenty-seven hauls made in this region resulted in catch rates ranging from 0.5 to 349 kg per hour of trawling. Eight families of elasmobranchs, 5 families of flatfish, 3 families of eels, 44 families of roundfish and 8 groups of invertebrates were present in the catches. Highest catch rates were obtained in the 15-37 m depth range followed by those in the 111-183, 74-110, 38-73 and 184-366 m depth ranges, respectively. Stingrays provided the highest catch rates and dominated catches from the 15-37 and 111-183 m depth ranges. Threadfin breams, which followed the stingrays in importance, were mainly taken in the 74-110 m depth range. Other important constituents of the fish catches were guitarfishes, croakers, and grunts. Relatively few invertebrates were caught in this region. Most of the shrimp were taken in the 184-366 m depth range.

Gulf of Oman

Of 27 hauls made in this region, 7 were not used in the catch analysis because the trawl was either badly torn or failed to perform satisfactorily. Catch rates from successful hauls ranged from 1 to 154 kg per hour of trawling. Represented in the catches were 5 families of elasmobranchs, 4 families of flatfish, 5 families of eels, 43 families of roundfish, and 7 groups of invertebrates. Highest catch rates in this region were obtained in the 74-110 m depth range, followed by those in the 38-73, 111-183, 15-37 and 184-366 m depth ranges, respectively. Threadfin breams yielded the highest catch rates and most were caught in the 74-110 and 111-183 m depth ranges. Only stingrays and croakers were of any importance in the remainder of the catches. Shrimp and other invertebrates were caught only in small quantities.

Arabia

Two of the 4 hauls made off Arabia resulted in extensive damage to nets from coral. The 2 successful hauls in the 38-73 m depth range yielded the highest catch rates for both Cruise 1 and Cruise 4 B. A 45-minute haul made at Station 270A (Fig. 7) yielded 834 kg of swimming crabs (Portunidae) and 771 kg of fish -- primarily grunts, stingrays, and cardinal fishes (Apogonidae). At Station 272A, a 30-minute haul yielded the largest catch of the entire survey -- 2,404 kg of stingrays and 45 kg of other fishes. Stingrays were the most important fish group taken with an average catch of 1,769 kg per hour of trawling. They were followed by swimming crabs with an average catch rate of 556 kg per hour of trawling. No shrimp were caught in this region.

Size of Organisms

Several families of roundfish were caught in substantial numbers, but the individuals were generally too small to be of commercial importance. The small mesh size of the trawl net used in these surveys contributed to the catch of small fish, some of which were only 4 cm in length. Undoubtedly, some of the families would not have been retained had the mesh size been larger.

Since the sizes of fish caught on Cruises 1 and 4B were similar, only the length frequencies and average weights of some that were frequently caught on Cruise 4B are shown in figures 8 and 9. Within the elasmobranchs group, guitarfishes ranged in weight from a few kilograms to 181 kg, sharks usually weighed but a few kilograms, and stingrays ranged from 0.5 to 205 kg. The stingrays taken in large numbers off the Arabian coast averaged about 18 kg each. Most of the eels were small except those that belong to the family Muraenesocidae which weighed from about 0.5 kg to about 9 kg each and reached lengths up to about 1.5 m. Most of the roundfish weighed less than 250 g with a small percentage of sea catfishes, croakers, grunts, sparids, and a few others that weighed up to a few kilograms each.

Shrimp ranged in size from more than 440 individuals per kilogram (heads on) to about 35 individuals per kilogram in the Arabian Sea, and on one occasion, 5 individuals to a kilogram in the Bay of Bengal. Squat lobster (Scyllaridae) which were caught frequently but only in small numbers usually weighed about 250 to 500 g per individual. The swimming crabs which were caught in large numbers off Arabia averaged about 22 individuals to a kilogram with carapace lengths ranging from 3.8 to 10.2 cm.

ENVIRONMENTAL FACTORS

Bathythermograph lowerings, surface and bottom temperatures, and bottom and surface water samples for salinity, phosphate and oxygen determinations were taken at nearly all of the trawl stations on Cruise 4B. Comparison of the catch data with some of the environmental data showed that the bottom oxygen concentrations were correlated with the catches ($r = 0.261$, $P < 0.05$) and that the bottom phosphate concentrations were inversely correlated with the catches ($r = -0.259$, $P < 0.05$). There were no significant correlations between the catches and the bottom salinities or the bottom temperatures.

Bottom temperatures decreased with increasing depth, the decrease being the greatest off India. Surface temperatures increased slightly progressing away from the coast. The surface salinities were highest in the Gulf of Oman and lowest off India. This was probably due to the fresh water run-off into the Gulf of Cambay and Kutch. Bottom oxygen levels were lowest off India and increased to the westward with the highest being observed off Arabia where the largest fish catches were taken. Tongues of mixed waters, as indicated by low phosphate concentrations (Fig. 10), intruded over the continental shelf just north and east of Karachi, in the northern part of the Gulf of Oman, along the eastern coast of Arabia, and off the India-West Pakistan border. In general, the larger trawl catches were made in areas of well mixed water. This is shown in figure 11 which illustrates the distribution of catches greater than 45.4 kg per hour of trawling that were obtained on Cruise 4B.

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TABLE I

Average catches in kilograms per hour of trawling, by depth range, obtained in the Andaman Islands region on Cruise 1 of the *Anton Bruun*. Dashes designate catches of less than 0.2 kg. (half a pound)

No. hauls	(1)	(2)
Depth in meters	38-73	74-110
Elasmobranch		
Carcharhinidae	3.6	
Dasyatidae		22.7
Flatfish		
Bothidae		-
Pleuronectidae		-
Roundfish		
Apogonidae		-
Carangidae	-	
Chaetodonitidae		-
Emmelichthyidae		-
Fistulariidae	-	
Gerridae	.9	
Labridae	-	
Leiognathidae	-	
Mullidae	-	-
Nemipteridae	-	.5
Ogcocephalidae		-
Pomacentridae		-
Priacanthidae		-
Scombridae		-
Serranidae		-
Synodontidae	-	-
Invertebrate		
Loliginidae		-

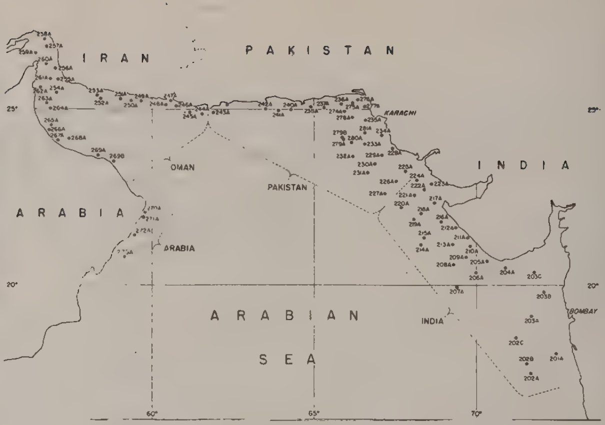
IRAN
PAKISTAN
KARACHI
INDIA
OMAN
PAKISTAN
ARABIA
ARABIA
ARABIAN SEA
INDIA
BOMBAY
25°
20°
60°
65°
70°

Fig. 4 Trawl stations on Cruise 4B of the ANTON BRUUN in the Arabian Sea, November 12 - December 10, 1963. Dashed lines separate the regions.

Fig. 2 Cod end being lifted over the sorting table.

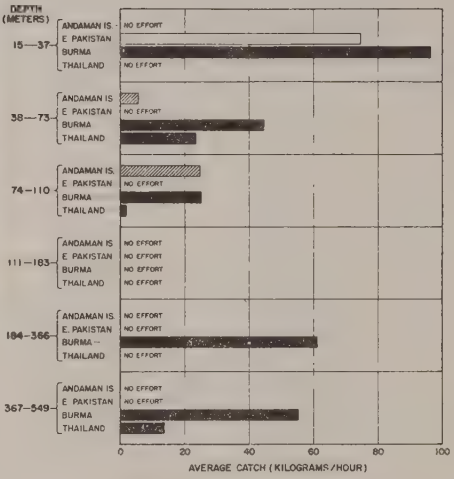

Fig. 5 Average catches in kilograms of fish and invertebrates per hour of trawling by depth ranges and by regions in the Bay of Bengal obtained on Cruise 1.

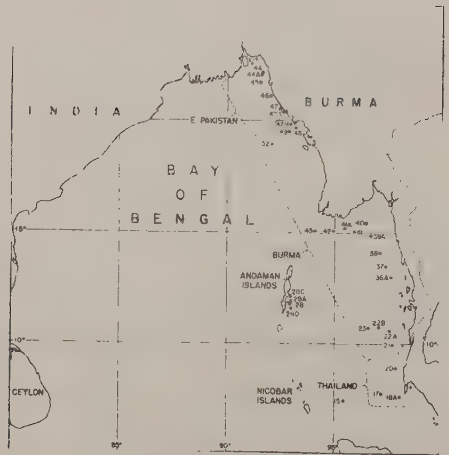
INDIA
BURMA
E PAKISTAN
BAY OF BENGAL
BURMA
ANDAMAN ISLANDS
NICOBAR ISLANDS
THAILAND
CEYLON
15°
10°
85°
90°
95°

Fig. 3 Trawl stations on Cruise 1 of the ANTON BRUUN in the Bay of Bengal, March 12 to April 11, 1963. Dashed lines separate the regions.

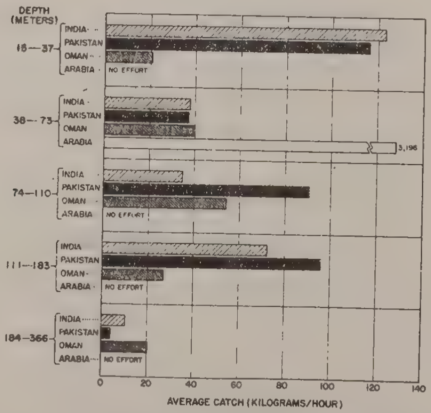

Fig. 6 Average catches of fishes and invertebrates in kilograms per hour of trawling by depth ranges and regions in the Arabian Sea obtained on Cruise 4B.

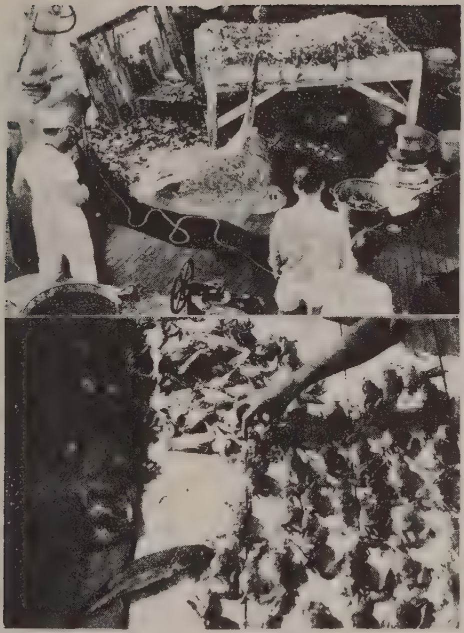

Fig. 7 Top photo shows the catch obtained at Station 270A on Cruise 4B of the BRUUN. Bottom photo shows the crabs which were caught in abundance.

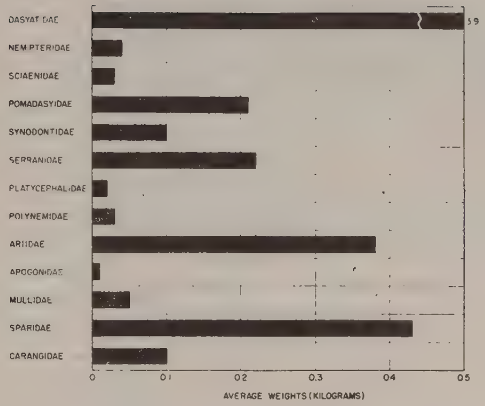

Fig. 9 Average weights of some fishes frequently caught on Cruise 4B.

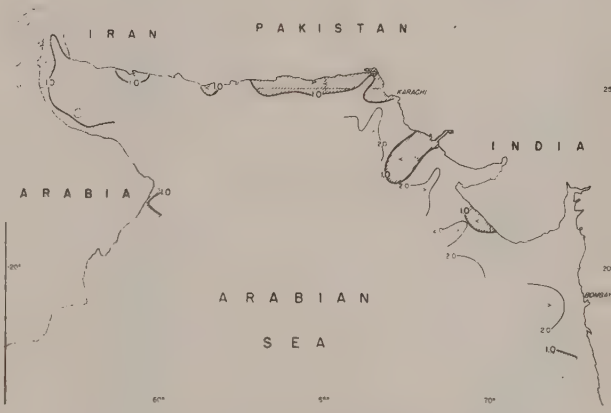
IRAN
PAKISTAN
KARACHI
INDIA
ARABIA
ARABIAN
SEA
1.0
2.0
20°
60°
65°
70°
BOMBAY

Fig. 10 Schematic illustration of bottom phosphate concentrations observed on Cruise 4B.

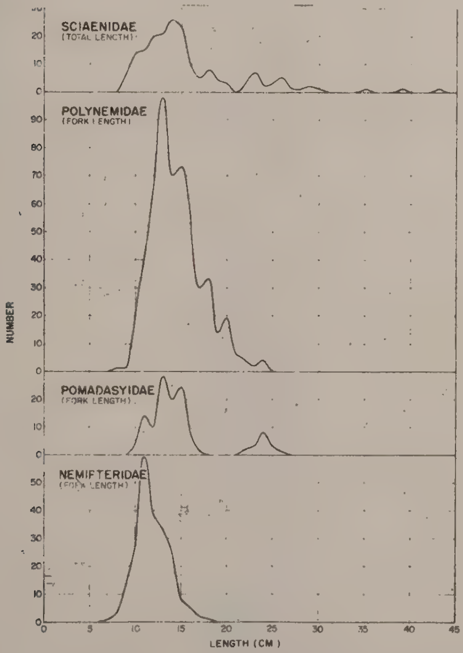

Fig. 8 Length-frequencies of some fishes frequently caught on Cruise 4B.

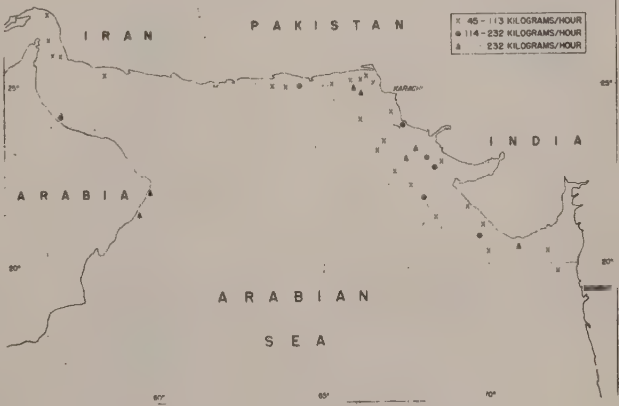
× 45 - 113 KILOGRAMS/HOUR
● 114 - 232 KILOGRAMS/HOUR
▲ 232 KILOGRAMS/HOUR
IRAN
PAKISTAN
KARACHI
INDIA
ARABIA
ARABIAN
SEA
25°
20°
60°
65°
70°

Fig. 11 Distribution of catches larger than 45.4 kg. per hour of trawling on Cruise 4B.

Table II

Average catches in kilograms per hour of trawling, by depth range, obtained in the Thailand region on Cruise 1 of the Anton Bruun. Dashes designate catches of less than 0.2 kg. (half a pound)

No. hauls	(1)	(1)	(1)
Depth in meters	38-73	74-110	367-549
Elasmobranch			
Rajidae			-
Flatfish			
Bothidae	.9		
Psettodidae	1.8		
Soleidae	-		
Eel			
Nemichthyidae			-
Unidentified	-		
Roundfish			
Apogonidae	-		
Brotulidae			-
Callionymidae	-		
Carangidae	.9		
Dactylopteridae	3.6		
Diodontidae		.5	
Drepanidae	-		
Emmelichthyidae	-	-	
Fistulariidae	-		
Grammicolepidae		-	
Labridae	-		
Macruridae			3.6
Mullidae	-		
Myctophidae			-
Nemipteridae	2.7		
Ogcocephalidae	-		
Ostraciontidae	-		
Peristediidae			-
Platycephalidae	.9		
Pomadasyidae	-		
Priacanthidae	-	.5	
Scolopsidae		-	
Scorpaenidae	.9		
Serranidae	-	-	
Stomiatidae			.9
Synodontidae	6.3	-	
Triacanthidae	-		
Zeidae			-
Unidentified			3.6
Invertebrate			
Crab	-		-
Polypodidae	.9		
Sepiolidae	-		
Shrimp	-		3.6

Table III

Average catches in kilograms per hour of trawling, b depth range, obtained in the East Pakistan region on Cruise 1 of the Anton Bruun. Dashes designate catch of less than 0.2 kg. (half a pound)

No. hauls	(6)
Depth in meters	15-37
Elasmobranch	
Carcharhinidae	.9
Dasyatidae	.5
Rhinobatidae	26.8
Sphyrnidae	.5
Torpedinidae	-
Flatfish	
Bothidae	.5
Soleidae	.5
Roundfish	
Apogonidae	-
Ariidae	5.0
Carangidae	.5
Clupeidae	2.3
Dactylopteridae	.5
Engraulidae	.5
Ephippidae	.9
Fistulariidae	-
Gerridae	-
Gobiidae	-
Harpodontidae	2.7
Lagocephalidae	-
Leiognathidae	.9
Lutjanidae	-
Monacanthidae	-
Mullidae	.9
Nemipteridae	.5
Pegasidae	-
Platycephalidae	.5
Polynemidae	5.0
Pomadasyidae	-
Sciaenidae	21.3
Scombridae	-
Scorpaenidae	-
Sillaginidae	-
Sparidae	-
Sphyraenidae	-
Syngnathidae	-
Synodontidae	.5
Tetraodontidae	-
Theraponidae	.5
Triacanthidae	-
Trichiuridae	-
Invertebrate	
Crab	.5
Loliginidae	.5
Scyllaridae	.5
Sepiolidae	-
Shrimp	2.3

Table IV

Average catches in kilograms per hour of trawling, by depth range, obtained in the Burma region on Cruise 1 of the *Anton Bruun*. Dashes designate catches of less than 0.2 kg. (half a pound)

No. hauls	(3)	(7)	(3)	(1)	(1)
Depth in meters	15-37	38-73	74-110	184-366	367-549
Elasmobranch					
Carcharhinidae	-			.9	3.6
Dasyatidae	41.3	5.9	.9		
Torpedinidae		-	-		
Flatfish					
Bothidae	-	-	.9	-	
Cynoglossidae	.9	2.7		-	
Pleuronectidae		-			
Psettodidae	-	1.4	-		
Soleidae		-	-		
Eel					
Unidentified	-	4.1		-	
Roundfish					
Apogonidae	-	.9	.9		
Ariidae	8.2	.5			
Balistidae		-	1.4		
Bembropsidae				.9	
Blenniidae		-			
Callionymidae			.5		
Carangidae	-	-	.5		
Carapidae			-		
Centriscidae		-			
Chaunacidae				-	
Chlorophthalmidae				18.1	.9
Clupeidae	-	-			
Dactylopteridae	-	.5	-		-
Eleotridae		-			
Ephippidae	.5		-		
Fistulariidae	-	.5	-		
Gerridae	-	-	-		
Gonostomidae					-
Harpodontidae	1.8				
Holocentridae			.5		
Leiognathidae	-	-			
Lophiidae		-	-		-
Lutjanidae		1.8	7.7		
Macruridae				.9	3.6
Monacanthidae		-	-		
Monodactylidae	-				
Mullidae	.9	.5	.9		
Myctophidae					-
Nempteridae	3.6	2.3	3.2		
Ogcocephalidae		-	-	-	
Ostraciontidae		-			
Parapercidae			-		
Pegasidae			-		
Platycephalidae	-	-	.5	-	
Polynemidae	6.8	-			
Pomacentridae			-		
Pomadasyidae	.5	1.8			
Priacanthidae		-		.9	
Rachycentridae	-				
Sciaenidae	16.3	9.1			
Scombridae			-		
Scorpaenidae	-	-	-	3.6	-
Serranidae		.5	1.4		
Sillaginidae	-				
Sparidae		.5			
Sphyraenidae		-			
Sternoptychidae					-
Stromateidae	-	-		1.8	
Synodontidae	.5	4.5	1.4		
Tetraodontidae	.9	-			
Theraponidae	-				
Triacanthidae	-	-		.9	
Trichiuridae	-	-		-	.9
Triglidae			.5		
Uranoscopidae	-	-	-		
Unident. Berycoid				.9	27.2
Unidentified	-	-		-	.9
Invertebrate					
Argonautidae			-		
Crab	-	-	.5		-
Loliginidae	-	-	.5		
Palinuridae		-		4.5	
Scallop	5.0	-			
Scyllaridae	-	-	.5		
Sepiolidae	.9	-	.5		
Shrimp	5.4	2.7	-	25.4	15.4
Stomatopoda	-	-			

Table V

Average catches in kilograms per hour of trawling, by depth range, obtained in the India region on Cruise 4B of the *Anton Bruun*. Dashes designate catches of less than 0.2 kg. (half a pound)

No. hauls	(10)	(7)	(5)	(4)	(2)
Depth in meters	15-37	38-73	74-110	111-183	184-366
Rays and sharks					
Dasyatidae	34.5	14.5			
Galeorhinidae			.5		
Rhinobatidae	3.6	-			
Torpedinidae	-				
Flatfish					
Bothidae	-	-	-	.5	
Cynoglossidae	-	-	-		
Pleuronectidae			-		
Soleidae	-	-	-	-	
Eel					
Congridae		-			-
Leptocephalus			-		
Muraenesocidae	4.1	-			
Nemichthyidae		-			
Roundfish					
Aluteridae	-	-			
Anthiidae			-		
Apogonidae	5.9	-	.5	-	2.3
Ariidae	1.8	.5	-		
Brotulidae		-			
Callionymidae		-	-		
Carangidae	.5	-	1.4	.5	
Chaetodontidae				-	
Champsodontidae			-	-	4.5
Chirocentridae	-				
Clupeidae	-				
Diodontidae				-	
Drepanidae	.5				
Engraulidae	1.4				
Fistulariidae	-	-	-	-	
Gadidae	-	-			
Gempylidae					.5
Gobiidae	-				
Harpodontidae	5.3				-
Lactariidae	-	-			
Lagocephalidae	-				
Leiognathidae	1.4	-	-	-	
Lutjanidae	.5		-		
Mullidae	.9	2.7	4.1		
Myctophidae					-
Nemipteridae	-	7.3	11.8	55.8	1.8
Ogcocephalidae			-	-	
Parapercidae			-	.5	
Platycephalidae	.5	1.4	5.9	-	
Plotosidae		-			
Polynemidae	18.1	.5	.5		
Pomadasyidae	1.4	-			
Priacanthidae			-		
Rachycentridae		.5			
Sciaenidae	27.7	-	.5		1.4
Scolopsidae		-	-	-	-
Scorpaenidae	-	-	-		
Serranidae	-	1.8	3.2	3.6	
Sparidae	1.8	1.4	.5		
Sphyraenidae		-	.5	-	
Stomiatidae					-
Stromateidae	-	-	-		-
Synanciidae	-	-	-	-	
Synodontidae	.5	3.2	2.3	9.1	
Theraponidae	-				
Trichiuridae	-	-	-		
Triglidae		.5	-	.9	
Uranoscopidae		-	-		
Invertebrate					
Caridea	1.8	-	-		
Crabs	-	-	.5		-
Loliginidae	.9	.5	.5	.9	
Penaeidae	6.3	.5	.9		-
Polypodidae		-	-	-	
Scyllaridae	.5	.9			
Sepiolidae	-	.9	1.8	-	
Stomatopoda	-	-			

Table VI

Average catches in kilograms per hour of trawling, by depth range, obtained in the West Pakistan region on Cruise 4B of the Anton Bruun. Dashes designate catches of less than 0.2 kg. (half a pound)

No. hauls	(12)	(1)	(8)	(4)	(2)
Depth in meters	15-37	38-73	74-110	111-183	184-366
Rays and sharks					
Carcharhinidae	.9	4.1			
Dasyatidae	43.1	1.4	.5	45.4	
Myliobatidae	-				
Rajidae	-				
Rhinobatidae	1.8		31.3	5.4	
Scylliorhinidae	.5		-	-	
Torpedinidae	-				
Unident. shark				-	
Flatfish					
Bothidae	-		-	-	
Cynoglossidae	.5			-	-
Psettodidae	-				
Soleidae	-		-	-	
Unident. flatfish					-
Eel					
Congridae	-		-	-	
Echelidae				-	
Muraenesocidae	1.8		1.8	.5	
Roundfish					
Apogonidae	-		-	-	.5
Ariidae	7.3	3.6	.5	-	
Callionymidae	-			-	-
Carangidae	1.4	3.6	8.2	-	
Cephalacanthidae	-				
Cepolidae			-		
Champsodontidae			-		.5
Chirocentridae	-				
Clupeidae	.9				
Drepanidae	2.7	-	-	-	
Echeneidae			-		
Engraulidae	.9		-	.9	
Fistulariidae	-		-		
Gadidae			-		-
Gerridae	-				
Harpodontidae				-	-
Lactariidae	8.6		.5		
Lagocephalidae	-	1.4	-		
Leiognathidae	2.3	-	.5		
Lutjanidae	-				
Mullidae	.5	.5	-		
Myctophidae					-
Nemipteridae	1.4	3.2	31.3	7.3	
Platycephalidae	.5	-	.5	-	
Polynemidae	4.1		2.7	4.1	
Pomadasyidae	9.5	12.2	.9	3.6	
Priacanthidae			-		
Rachycentridae	.9		.5		
Sciaenidae	19.0		6.8	10.0	.5
Scolopsidae			-	16.3	
Scombridae	-				
Scorpaenidae	-			-	
Serranidae	-		1.4	.5	
Sparidae	3.6	3.2	-		
Sphyraenidae	.9		-		
Stromateidae	.5		-	.5	
Synanciidae	-				
Synodontidae	1.8	3.6	.9	-	
Tetraodontidae	.9		-		
Theroponidae	1.4				
Thunnidae			-		
Trichiuridae	.5		-	-	
Triglidae	-		-	.5	
Uranoscopidae	-		-		
Invertebrate					
Argonautidae			-		
Crabs			-	-	
Loliginidae	.9		.5	-	
Palinuridae	-			-	
Penaeidae	.5		-	.5	2.7
Scyllaridae	-				
Sepiolidae	-		.9	-	
Stomatopoda	-				

Table VII

Average catches in kilograms per hour of trawling, by depth range, obtained in the Gulf of Oman region on Cruise 4B of the Anton Bruun. Dashes designate catches of less than 0.2 kg. (half a pound)

No. hauls	(3)	(5)	(6)	(2)	(4)
Depth in meters	15-37	38-73	74-110	111-183	184-366
Rays and sharks					
Carcharhinidae			4.5		
Dasyatidae		26.8		.9	
Rhinobatidae	.5		-		
Scylliorhinidae			.5		1.8
Torpedinidae					-
Flatfish					
Bothidae		.5	-	.5	
Cynoglossidae				1.8	-
Pleuronectidae			-		
Psettodidae	.5	-	-		
Eel					
Congridae		-		-	.9
Leptocephalus				-	
Muraenesocidae		1.8	.5		.9
Nemichthyidae					-
Nettastomidae					-
Roundfish					
Apogonidae	-		-	-	2.7
Ariidae	1.8	.9	3.2		
Brotulidae					-
Callionymidae				-	-
Carangidae	.5	.5	7.3		
Champsodontidae		-	-	-	-
Clupeidae	-		-		
Drepanidae	.5	.5			
Echeneidae	.5				
Engraulidae	-	-			-
Fistulariidae	-	-	-		
Gadidae	-	-	-	-	
Gempylidae					-
Gerridae	-				
Gobiidae				-	
Harpodontidae					.5
Holocentridae					.9
Lactariidae	-				
Lagocephalidae	-		.5		
Leiognathidae	-	.5	.5		
Lutjanidae			5.0		
Menidae	-				
Mullidae	2.7	-	.5		
Myctophidae				-	
Nemipteridae	2.3	.9	13.6	10.9	.9
Ostraciontidae			-		
Platycephalidae	.5	.5	.9		
Polynemidae		-		.5	
Pomadasyidae	2.7	.9	2.7		-
Priacanthidae			.9		
Rachycentridae		1.8			
Sciaenidae	-	-	-	3.6	10.0
Scolopsidae			-	3.2	.5
Scorpaenidae					-
Serranidae	-	.5	3.6	.5	.5
Sparidae		.5	1.8		
Sphyraenidae			.5		
Stromateidae				-	-
Synanciidae		-			
Synodontidae	4.1	2.3	2.3		
Trichiuridae				-	.5
Triglidae	-	-	-	.5	
Uranoscopidae		-	-		
Invertebrate					
Crabs	-		3.6	-	-
Loliginidae	.5	-	.9		.5
Penaeidae	.9		-	.9	3.6
Polypodidae			-	-	
Scyllaridae	-	.5			
Sepiolidae	-	-	.9	.9	.5
Stomatopoda			-		-

Table VIII.

Average catches in kilograms per hour of trawling, by depth range, obtained in the Arabia region on Cruise 4B of the Anton Bruun. Dashes designate catches of less than 0.2 kg. (half a pound)

No. hauls	(2)
Depth in meters	38-73
Rays and sharks	
Dasyatidae	2040.8
Flatfish	
Bothidae	-
Cynoglossidae	-
Roundfish	
Apogonidae	76.2
Ariidae	3.6
Carangidae	9.5
Cephalacanthidae	1.8
Gerridae	1.8
Lagocephalidae	1.8
Leiognathidae	1.8
Nemipteridae	28.6
Platycephalidae	3.6
Pomadasyidae	346.9
Sparidae	4.1
Synanciidae	1.8
Synodontidae	12.7
Theraponidae	3.6
Triglidae	12.7
Uranoscopidae	-
Invertebrate	
Crabs	641.7
Loliginidae	-

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A BACTERIAL BASIS FOR THE GROWTH OF ANTIBIOTIC-TREATED BIVALVE LARVAE

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ABSTRACT

Routine addition of the proprietary antibiotic formulation "Combistrep" (dihydrostreptomycin-streptomycin sulfates) to larval cultures of clams, Mercenaria mercenaria, or oysters, Crassostrea virginica, usually results in a significant increase in growth rate of larvae. It had been assumed that this increase was effected by the elimination or suppression of bacterial flora, but plate counts show that the total number of marine bacteria increases in almost direct proportion to the added Combistrep up to 2,000 parts per million. Bacteria-free clam larvae showed no growth when cultured in autoclaved sea water to which Combistrep had been added. In Combistrep-treated cultures inoculated with a mixed flora of marine bacteria, the larvae showed significant growth, while cultures that received the bacterial inoculum but no Combistrep showed little or no growth. These results suggest that the antibiotic-induced bacterial flora in the Combistrep-treated cultures may be utilized by larvae as a food source.

INTRODUCTION

Since the development of methods of rearing larvae of clams, Mercenaria mercenaria, and oysters, Crassostrea virginica, the role of bacteria and dissolved substances in their nutrition has been a matter of conjecture. It has been shown that supplemental live algal foods are primarily responsible for growth and development of these larvae (Davis and Guillard, 1958). On occasion, however, other factors have been observed or suspected to play an important part in nutrition of larvae. Davis and Chanley (1956) reported an increase in the growth rate of clam and oyster larvae on the addition of several vitamins and antibiotics but offered no suggestion on how the increased growth was achieved. Carriker (1956) reared clam larvae to metamorphosis on an extract of cereal, Pablum, and concluded that the good growth of larvae was the result of increased microbial populations stimulated by the addition of the Pablum filtrate. Loosanoff, Davis, and Chanley (1955) stated that clam larvae seem able to utilize sulfur bacteria. Coe (1947) and Rodinca (1948) believed that bacteria played a part in the diet of adult mollusks. On the other hand, Davis (1953) fed pure cultures of nine species of marine bacteria to larval oysters with no success. Loosanoff, Davis, and Chanley (1955) stated that lack of success in growing oyster larvae on several species of marine bacteria contradicts the generally accepted view that marine bacteria constitute an important part of the oyster diet.

The present paper reports experiments which show the growth-producing effect on clam and oyster larvae of a commercial antibiotic preparation Combistrep[1] (dihydrostreptomycin and streptomycin sulfates). It is furthermore demonstrated that the increase in growth of larvae is associated with a stimulation of marine bacterial populations by the Combistrep. This antibiotic preparation was originally used at the Milford laboratory in an attempt to prevent mortalities of larvae resulting from bacterial diseases, and its effect in increasing growth rates of bivalve larvae was first noted by Chanley (personal communication).

MATERIALS AND METHODS

Methods of conditioning and spawning adult bivalves and rearing larvae in the laboratory have been described in detail (Loosanoff and Davis, 1950). To determine effects of Combistrep on clam and oyster larvae, fertilized eggs were cultured 48 hours at concentrations of approximately 30 per ml in filtered ultraviolet-light-treated sea water. Forty-eight-hour veliger larvae were then collected on stainless steel screens and diluted to a known volume. After the number of larvae per unit volume was determined, appropriate volumes were used to set up experimental cultures with about 10 larvae per ml.

The culture medium, including test materials, was renewed every second day by collecting the larvae on a stainless steel screen and transferring them to new media. Temperatures were held to 24 ± 1 C throughout. After 10 days' exposure to the experimental conditions clam veligers were sampled quantitatively. Oyster veligers were similarly sampled after 12 days. Effect of experimental treatment on growth of larvae was determined by measuring the long axis of 50 clam or 100 oyster larvae. The generally uniform size of clam larvae permits good accuracy with the lesser sample size.

Methods used in determining the effects of Combistrep on marine bacteria and the effects of the stimulated bacterial populations on bivalve larvae are included briefly within the respective result sections.

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[1] Reg. U. S. Pat. Off. Chas. Pfizer & Co., Inc.

Combistrep is a proprietary compound of Chas. Pfizer & Co., Inc., and has the following composition:

dihydrostreptomycin base (as sulfate)	125 mg/cc
streptomycin base (as sulfate)	125 mg/cc
phenol	0.25%
sodium citrate	1.3%
sodium bisulfate	0.2%
water	77.4%

RESULTS

A compilation of data from experiments over the past several years demonstrates that both clam and oyster larvae receiving Combistrep have consistently shown more rapid growth than larvae in comparable cultures that did not receive Combistrep (Figs. 1 and 2). At concentration ranges of 100 to 300 parts per million (ppm), Combistrep generally increased the rate of growth of clam larvae by more than 100% in cultures not receiving a supplemental feeding of algae (Fig. 1). Growth of these untreated, unfed larvae varied considerably, i.e., the mean length at 10 days varied from about 115 to about 148μ. Such differences in growth are certainly due to variations in the amount of food present in the filtered ultraviolet-light-treated sea water. In all cases, however, above average growth in the untreated, unfed cultures was accompanied by a correspondingly more rapid growth of larvae in the Combistrep-treated unfed cultures.

Clam larvae receiving 200 to 400 ppm of Combistrep and no supplemental algal feeding when reared beyond the usual 10-day experimental period in all cases grew to metamorphosis with negligible mortality within 20 days at 24 C. In all such instances, of course, it required a longer time for these larvae to reach metamorphosis than for larvae receiving algal food supplements, but untreated, unfed larvae in parallel cultures never progressed beyond 140μ in length.

Combistrep also increased growth of clam larvae receiving live flagellates as food (Fig. 1). The increase in the growth increment averaged about 25μ at 12 days of age at optimal Combistrep concentrations. This was about a 25% increase in growth over larvae fed live flagellates without Combistrep. The optimum concentrations of Combistrep appeared to be higher in cultures receiving algal foods than in those not receiving the algae.

Growth of oyster larvae was increased nearly 100% by the addition of Combistrep at concentrations between 200 and 300 ppm

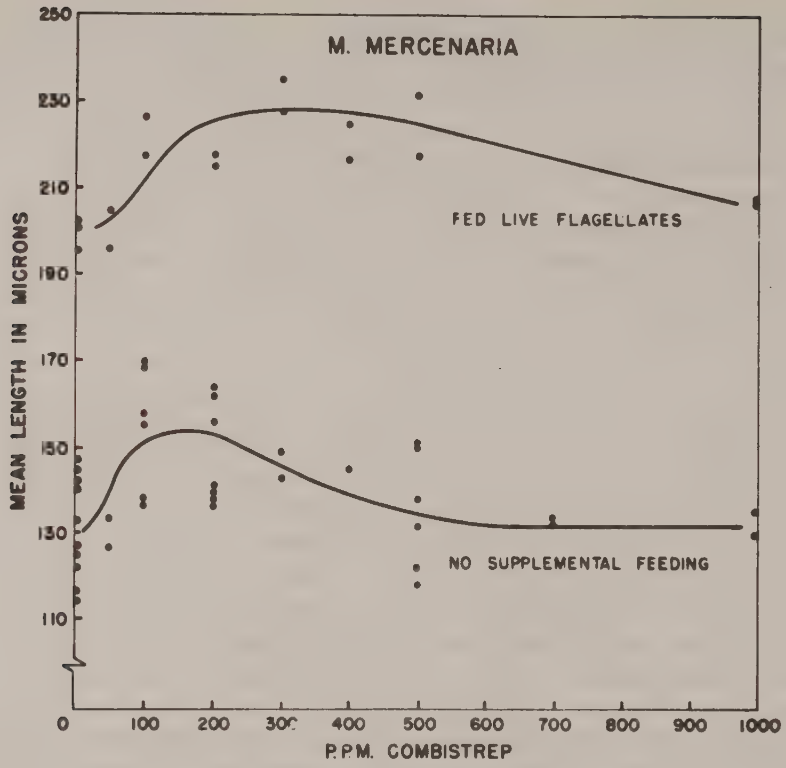

Fig. 1. Mean lengths of clam, M. mercenaria, larvae at 12 days of age receiving several dosage rates of Combistrep, with and without supplemental algal feeding. Data are a composite of several experiments which included Combistrep-treated cultures, together with suitable untreated controls. Each point represents a mean length of 50 larvae from a single population of approximately 10,000 larvae.

(Fig. 2). Figure 2 represents a composite of Combistrep-treated cultures, some of which received algal food supplements while others did not. Controls not receiving Combistrep are included in all cases, however. Because of the sensitivity of oyster larvae to variations in algal food quality, it is often difficult to distinguish larvae receiving algal food from those not receiving the food. The composite of mean lengths of fed and unfed larvae, however, clearly shows the value of Combistrep in increasing growth rates.

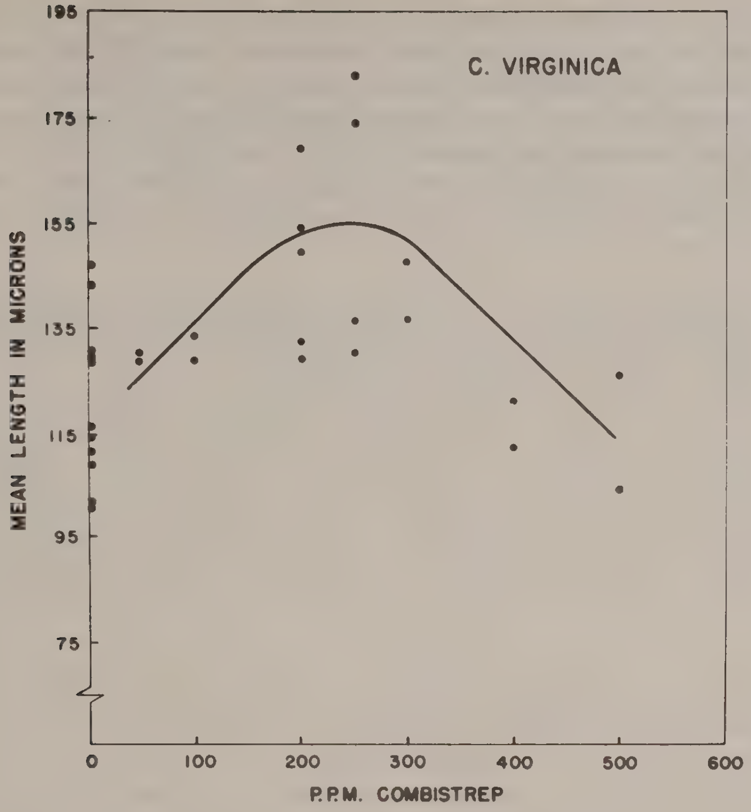

Fig. 2. Mean lengths of oyster, C. *virginica*, larvae at 14 days of age receiving several dosage rates of Combistrep. Data are a composite of several experiments which included Combistrep-treated cultures, together with suitable untreated controls. Each point represents a mean length of 100 larvae from a single population of approximately 10,000 larvae.

Effects of Combistrep on Bacterial Populations

It was noticed in the above experiments that, although Combistrep did help to prevent mortalities in cultures of clam and oyster larvae, the bacterial population of larval cultures treated with Combistrep and some other antibiotics became actually higher than bacterial populations in untreated cultures. Experiments were then designed to determine the effect of different concentrations of Combistrep on bacterial populations in sea water.

One-liter cultures of filtered ultraviolet-light-treated sea water were set up and given several different concentrations of Combistrep but without larvae and algal food. After 48 hours at 24 ± 1 C samples for plate counts of bacteria were taken. The 48-hour cultures were plated at several dilutions using standard plating techniques on Trypticase Glucose Yeast Extract Agar made up with sea water. Bacterial colonies were counted; no attempt was made to determine the species of bacteria represented.

Increasing dosages of the sterile antibiotic resulted in almost directly proportional increases in bacterial numbers (Fig. 3). This

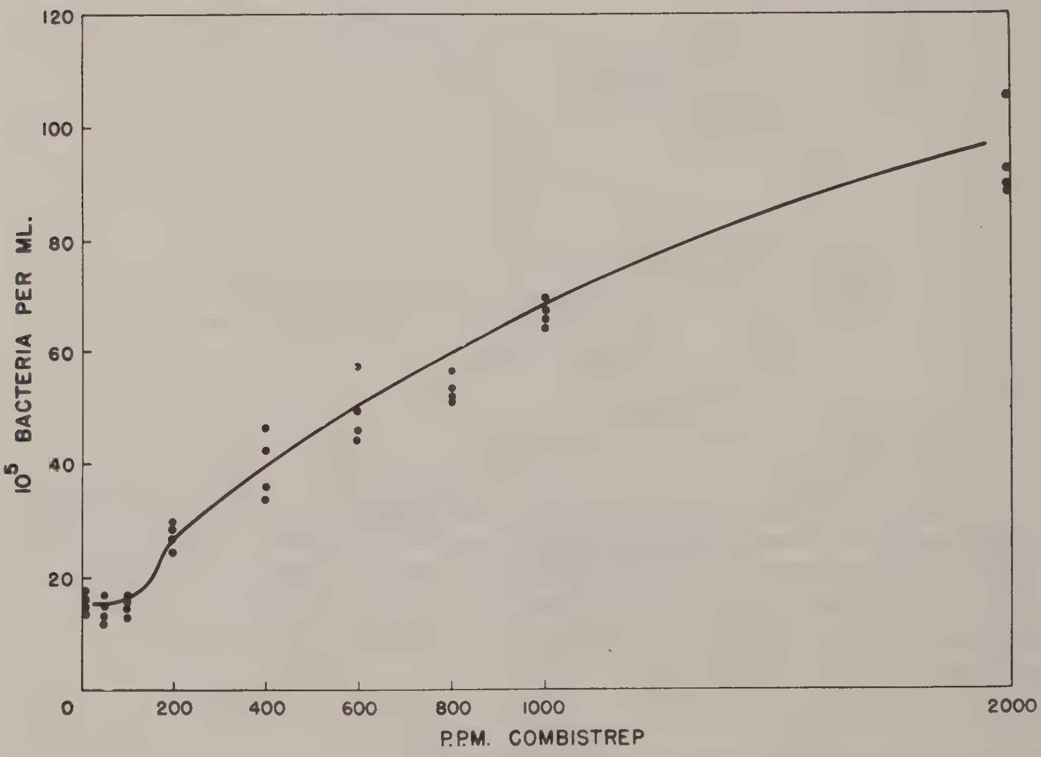

Fig. 3. Numbers of bacteria per ml of filtered sea water 48 hours after application of several concentrations of Combistrep. Duplicate sea water cultures were used at each test concentration. Points represent each of duplicate plate counts made of each sea water culture.

effect was not noted at the lowest concentrations (50 to 100 ppm). At concentrations of Combistrep that have been especially beneficial to larvae (200 to 400 ppm), there was approximately a two-fold increase in bacterial numbers over Combistrep-free cultures. Although the actual number of bacteria differed somewhat from experiment to experiment, the percentage increase with increasing dosages of Combistrep remained relatively constant.

Effect of Bacteria on Growth of Larvae

At this point it was important to determine whether the bivalve larvae were deriving benefit from the Combistrep directly or possibly from the increased bacterial populations that resulted from its addition to sea water. To do this we were eventually able to compare growth of larvae in aseptic and in bacterized Combistrep-treated cultures. Before we had developed methods for obtaining sterile larvae for aseptic cultures, however, several experiments were run in an attempt to correlate the rate of growth of larvae with the number of bacteria present.

It was postulated that if bacteria here were important in growth, then larvae receiving Combistrep and sea water with a fully developed bacterial population should grow more rapidly than larvae receiving Combistrep and sea water which were sterile. Consequently, non-sterile clam larvae receiving Combistrep were reared in sea water (1750 larvae in 500 mls) pretreated as follows:

1. Autoclaved and aged one week with sterile Combistrep added at the time of addition of water to cultures of larvae (sterile water supply).

2. Autoclaved, then aged one week after Combistrep plus a non-sterile sea water inoculum had been added (fully developed initial bacterial populations).

Larvae in control cultures, not receiving Combistrep, were reared in sea water with the following pretreatment:

1. Autoclaved, then aged one week.

2. Autoclaved, then aged one week after a non-sterile sea water inoculum had been added.

3. Autoclaved with live flagellate food added at the time of feeding to cultures of larvae.

The water in each culture was completely renewed every 24 hours and temperatures held to 20 C to minimize buildup of bacteria in treatments receiving the initially sterile water supplies. Duplicate cultures were used to test each treatment in each of the three replicate experiments. Results are shown as mean lengths of larvae after eight days of culture (Table 1). Mortality of larvae in all cases was negligible and thus is not included.

In the first experiment larvae grown in the presence of Combistrep with a fully developed initial bacterial population reached a mean length of 149.65µ, while those grown with Combistrep and sea water which were initially sterile reached only 117.90µ. Control cultures, i.e., those reared in sterile sea water and those kept in aged water plus the bacterial inoculum, also showed poor growth. Although the 149.65µ mean length was appreciably less than the 175.15µ mean length attained by larvae receiving live flagellates as food, it represents a significantly faster rate of growth than was achieved in control cultures.

The second experiment (Table 1), although conducted in exactly the same manner as the first, produced quite different results. In this trial 500 ppm Combistrep actually retarded clam growth, both when given with a sterile water supply and with a fully developed bacterial population. Since 500 ppm Combistrep is above an optimum dosage for clam larvae (Fig. 1), variable results might be expected. Growth was not reduced in a control culture within this experiment given only 250 ppm Combistrep. In a third trial Combistrep concentrations were adjusted to 250 ppm, which is a more nearly optimum concentration for clam larvae.

At 250 ppm (Experiment 3, Table 1) Combistrep-treated sea water with a fully developed initial bacterial population again produced good growth of clam larvae. Larvae kept in this water attained a mean length of 166.53µ, a length not much smaller than the 189.05µ achieved by larvae receiving live flagellate food. Larvae receiving sterile Combistrep and sterile sea water showed some growth (135µ mean length), while larvae kept in the sterile sea water and those kept in non-sterile sea water without Combistrep showed very little growth (121.20 and 116µ mean lengths, respectively).

Plate counts were made immediately after a change of sea water and again 24 hours later in this experiment to determine the typical numbers of bacteria at 0 and at 24 hours with each treatment (Table 2).

Table 1. The effect of several sea water treatments on the growth of non-sterile clam larvae. Larvae were cultured for 8 days at 20 C with water supplies renewed every 24 hours.

Sea water culture supply	Mean length (μ)		
	Exp. #1	Exp. #2	Exp. #3
Autoclaved (sterile)	113.00 ± 0.84[1]	121.25 ± 1.30	120.20 ± 0.83
Autoclaved + Combistrep (500 ppm)	117.90 ± 0.76	118.25 ± 0.94	No trial
Autoclaved + Combistrep (250 ppm)	No trial	126.65 ± 1.40	135.00 ± 1.18
Autoclaved + non-sterile inoculum (aged)	122.90 ± 1.09	125.55 ± 1.42	116.00 ± 0.77
Autoclaved + non-sterile inoculum + Combistrep (500 ppm) (aged)	149.65 ± 1.09	119.15 ± 1.66	No trial
Autoclaved + non-sterile inoculum + Combistrep (250 ppm) (aged)	No trial	No trial	166.53 ± 2.73
Autoclaved + flagellate food supplement	175.15 ± 1.68	190.35 ± 2.21	189.05 ± 2.64

[1] Indicates 95 per cent confidence limits, ± 1.98 SEm

Table 2. Numbers of bacteria present in non-sterile larval clam cultures receiving different treatments (Experiment 3, Table 1). Counts were made at times of water renewal (0 hours) and at the end of each change cycle (24 hours).

Sea water culture supply	Bacteria per ml	
	0 Hours	24 Hours
Autoclaved	19,000—21,000	550,000—580,000
Autoclaved + Combistrep	33,000	4,000,000
Autoclaved + non-sterile inoculum (aged)	50,000—100,000	65,000—150,000
Autoclaved + non-sterile inoculum + Combistrep (aged)	100,000—180,000	145,000—500,000

Although bacterial numbers were low at 0 hours in the cultures receiving the sterile water (19,000 to 33,000 bacteria per ml), there was a rapid buildup in the cultures by 24 hours (550,000 to 4,000,000 bacteria per ml). On the other hand, numbers of bacteria were initially high in cultures receiving the non-sterile water treatments (50,000 to 180,000 per ml) and showed a slower rate of increase in these cultures (65,000 to 500,000 per ml) at 24 hours. The aged sea water that had received the non-sterile inoculum plus Combistrep had considerably more bacteria per ml, both at 0 and at 24 hours, than the aged sea water that had the bacterial inoculum only. These results are in general agreement with experiments in which we determined the effect of Combistrep on the number of bacteria in sea water as previously described.

In subsequent experiments bacteria-free larvae were used to test the effect of Combistrep in aseptic vs. non-sterile cultures. Fertilized clam eggs collected on sterile stainless steel screens were washed several times with autoclaved sea water. These eggs were then permitted to develop into 48-hour veliger larvae in the trivalent antibiotic solutions described by Guillard (1959). Five to ten of these sterile larvae were then transferred aseptically to 10 ml of autoclaved sea water in each of 16 test tubes for each of the following treatments:

1. No treatment (sterile control)
2. 250 ppm sterile Combistrep (Combistrep only)
3. 0.1 ml non-sterile sea water (bacteria only)
4. 250 ppm sterile Combistrep + 0.1 ml non-sterile sea water (Combistrep + bacteria).

After sterile larvae had been added cultures were held 11 days at room temperature. Sterility tests in sea water-thioglycollate were run on treatments 1 and 2 (above) at the end of the experimental culture period. Larvae in all vials were then killed and length measurements were taken of all larvae that had survived the test period.

Of several such experiments to measure growth of clam larvae receiving Combistrep under septic and aseptic conditions, only one was successful. In this experiment many of the culture tubes of the sterile groups remained sterile to the end of the test period, permitting valid measurement of the effect of treatment. Larval survival in this experiment was variable, but due to the low initial larval density survival did not appear to affect growth rates. The results expressed as mean lengths of larvae are listed in Table 3. In addition to the four original experimental treatments, two additional categories developed. These were the mean lengths of larvae from several cultures of the two originally sterile treatments which proved non-sterile by the end of the culture period. Although all larvae grew poorly, differences in mean lengths between treatments were highly significant statistically. An analysis of variance gave an F value of 21.82, indicating an overall difference of means significant far greater than the 99% confidence level (Snedecor, 1962).

Tests of significance of differences between individual treatments within this experiment showed that (a) mean length of sterile larvae (102.82μ) was not significantly different (at the 99% confidence level) from sterile larvae receiving Combistrep (103.68μ); (b) sterile larvae (102.82μ) did not differ significantly from those receiving the non-sterile inoculum but no Combistrep (105.54μ); (c) larvae receiving Combistrep plus the non-sterile inoculum (110.84μ) were significantly larger (at the 99% confidence level) than either those receiving Combistrep under sterile conditions (102.82μ) or those that had received only the non-sterile inoculum (105.54μ).

Table 3. Mean lengths of clam larvae after 11 days of culture receiving several different treatments

Treatment	Mean length (μ)
1. Sterile	102.82
2. Sterile + 250 ppm Combistrep	103.68
3. Bacterized non-sterile	105.54
4. Non-sterile + 250 ppm Combistrep	110.84
1a. Sterile (contaminated)	106.14
2a. Sterile + 250 ppm Combistrep (contaminated)	108.53

Also notable was the fact that the larvae receiving the sterile-Combistrep treatment, which accidentally became contaminated (108.53μ), were significantly larger than the other replicates within the treatment which remained sterile to the end of the culture period (103.68μ).

DISCUSSION AND CONCLUSIONS

The mechanism by which Combistrep induces greater bacterial populations in sea water can only be speculated upon at this time. Experiments thus far have only measured increase in gross numbers of bacteria without regard to possible species selection. It is possible that Combistrep is acting to inhibit certain toxin-producing species, thus allowing greater total numbers. The possibility of the minimal quantity of citrate present in dilute Combistrep acting as an energy source seems remote.

The series of experiments in which non-sterile clam larvae were exposed to Combistrep-treated sea water both sterile and with fully developed bacterial populations initially present indicated that the rate of growth of larvae was associated with the number and probably the species of bacteria present and suggested that the larvae were using these bacteria as foods. In the two experiments in which Combistrep was beneficial to larvae (Exps. 1 and 3, Table 1), those larvae cultured in Combistrep-treated water with high initial populations of bacteria present in each case showed markedly greater growth than those receiving the initially-sterile water plus Combistrep. Although clam cultures receiving Combistrep with low initial bacterial numbers contained appreciable populations of bacteria by the end of the 24-hour water change cycle, there undoubtedly were significantly fewer bacteria present in these cultures throughout most of the 24-hour change cycle than in those receiving Combistrep with initially high bacterial populations. The fact that larvae in cultures receiving the bacterized aged water without Combistrep showed poor growth even though there were considerable bacterial populations present, throughout, would indicate that Combistrep was selecting and accelerating the growth of only certain beneficial species of bacteria.

The experiment using bacteria-free larvae showed that clam larvae in bacterized Combistrep-treated cultures grew, whereas those kept in sterile Combistrep-treated cultures and those kept in sterile, non-treated cultures showed little or no growth. This again demonstrated that it was the bacteria associated with the Combistrep treatment, not the Combistrep, itself, that caused the more rapid growth of bivalve larvae. Again, larvae in bacterized cultures that did not receive Combistrep showed less growth than in similar cultures containing Combistrep. This supports the above contention that the Combistrep-induced bacteria are perhaps of preferential utility to the larvae.

It is conceivable that the increased numbers of bacteria may at times be too great (over 500 ppm Combistrep). Such a biological mass might nullify beneficial effects by the creation of adverse environmental conditions for the larvae, such as reduction of dissolved oxygen, creation of toxic metabolites, etc. The variable results measured at 500 ppm Combistrep between experiments (Table 1) may be the result of this.

These studies, of course, do not show beyond all doubt that bacterial populations are utilized directly as food by bivalve larvae but do very definitely associate increased and probably selected bacterial populations with larval growth. As we learn more about these relationships, it may be possible to control bacterial populations to such an extent that they may become generally useful in future shellfish hatcheries, possible circumventing the presently difficult culture of relatively fastidious live algal food cells.

SUMMARY

1. Routine addition of the proprietary antibiotic formulation, "Combistrep" (dihydrostreptomycin-streptomycin sulfates) to cultures of clam or oyster larvae has consistently resulted in 25 to 100 per cent increases in the rate of growth of the larvae.

2. The addition of sterile Combistrep to filtered ultraviolet-light-treated sea water has produced an increase in numbers of bacteria roughly proportional to the concentration of Combistrep.

3. Tests with non-sterile Combistrep-treated cultures showed that clam larvae grew faster in Combistrep-treated cultures with a high initial bacterial count than in cultures with a low initial count.

4. In bacteria-free cultures the addition of Combistrep did not increase the rate of growth of clam larvae.

5. All data indicate that the increased rate of growth of larvae receiving Combistrep treatment is associated with the increase in numbers of a possibly selected group of bacteria.

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SIZES OF ALBACORE AND BIGEYE, YELLOWFIN, AND SKIPJACK TUNAS IN THE MAJOR FISHERIES OF THE PACIFIC OCEAN

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Honolulu, Hawaii

ABSTRACT

Most bigeye tuna (Thunnus obesus) taken by the Japanese longline fishery are about 80 to 150 cm. long in the North Pacific (the larger fish are caught east of long. 165° E.) and about 100 to 160 cm. long in equatorial waters. Males predominate among the larger fish. Catches during exploratory longline expeditions to the equatorial Pacific suggest that bigeye tuna tend to increase in size from west to east. Bigeye tuna caught near the surface in both the eastern and western Pacific are smaller than those caught by longline. Albacore (T. alalunga) in the Japanese longline fishery in the North Pacific are mostly 60 to 110 cm. long; there tends to be an alternate-year cycle in the positions of dominant length modes. In the tropical Pacific longline fishery, there is no east-west size gradient (as with bigeye tuna), but there is a north-south one; the larger fish are taken in warmer waters. Albacore landed at American Samoa range from about 70 to 110 cm. Albacore taken in surface fisheries are smaller than those caught on longline. Yellowfin tuna (T. albacares) in the western equatorial Pacific longline fishery display modal groups at about 90 to 100 and 120 to 130 cm. Exploratory expeditions to the equatorial Pacific show that yellowfin tuna from the open sea are slightly larger than those caught within 80 miles of land. Catch rates are generally higher near shore. Males outnumber females and attain a larger size. Average size increases from west to east. Yellowfin tuna taken by the live-bait and purse seine fishery of the eastern tropical Pacific are smaller than those caught on longline, averaging about 70 cm. Skipjack tuna (Katsuwonus pelamis) between about 40 and 70 cm. are taken off Japan and near Palau, Trust Territory of the Pacific Islands. In Hawaii, modal lengths of 35, 50, and 70 cm. are common in winter, 45 and 70 cm. in summer. Skipjack tuna longer than 60 cm. invariably constitute more than half the catch during at least one summer month. Skipjack tuna taken in the eastern tropical Pacific are usually much smaller than the large fish that dominate the Hawaiian summer catch.

INTRODUCTION

The size structure of tuna stocks in the Pacific Ocean may be described through either of two approaches. One is to construct composite weight- or length-frequency distributions for the major fishing areas. Such an approach is advantageous in that it affords a quick impression of the general size of the fish in an exploited stock, but it fails to indicate the continually changing nature of these size compositions. A second approach is to present individual frequency distributions for samples of each species of tuna caught in each area. These figures reveal, as composite distributions cannot, the effects that several factors have on the size composition of tuna stocks. The size composition of samples of four species of tuna, the bigeye tuna (*Thunnus obesus*), the albacore (*Thunnus alalunga*), the yellowfin tuna (*Thunnus albacares*), and the skipjack tuna (*Katsuwonus pelamis*), are discussed here in light of the possible influence on size of such factors as (1) area and season of capture, (2) fishing method, (3) schooling behavior, and (4) sex of the fish.

SIZE DISTRIBUTION OF BIGEYE TUNA

Major Japanese longline fishing areas for bigeye tuna are in the western North Pacific and across the entire equatorial Pacific. Bigeye tuna are also taken by longline gear around the Hawaiian Islands, and by live-bait fishing near Japan and off Baja California and northern South America (Alverson and Peterson, 1963).

Japanese North Pacific Longline Fishery

Kamimura and Honma (1953) measured bigeye tuna taken north of lat. 26° N. between long. 130° E. and 165° W. during the 1948-52 fishing seasons. Most were about 80-150 cm. long, the total range being 53-192 cm. (fig. 1). Modal groups were at about 85-96, 117-124, and 149-152 cm. in the even-numbered years, but in odd-numbered years lengths of 93-100, 105-113, and 133-140 cm. were most common. The authors also noticed that modes made up of groups of smaller fish predominated in the areas west of long. 165° E., whereas modes composed of larger bigeye tuna characterized fish east of that longitude (fig. 2).

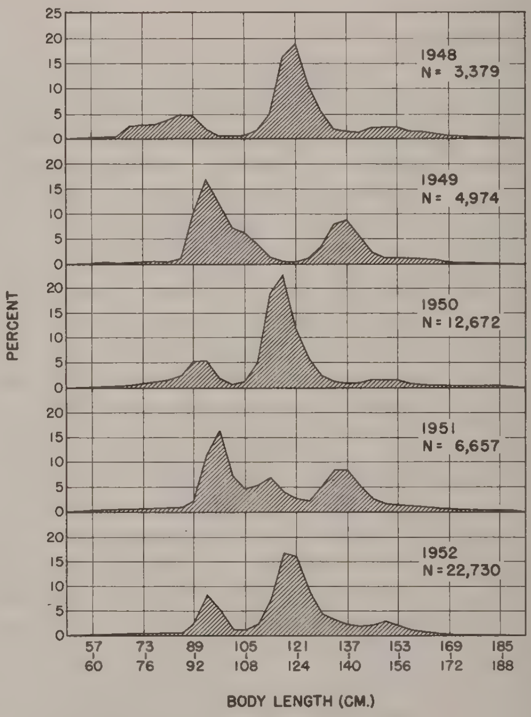

Figure 1.--Length frequencies of bigeye tuna taken during the 1948-52 seasons in the Japanese North Pacific longline fishery. Based on Kamimura and Honma (1953).

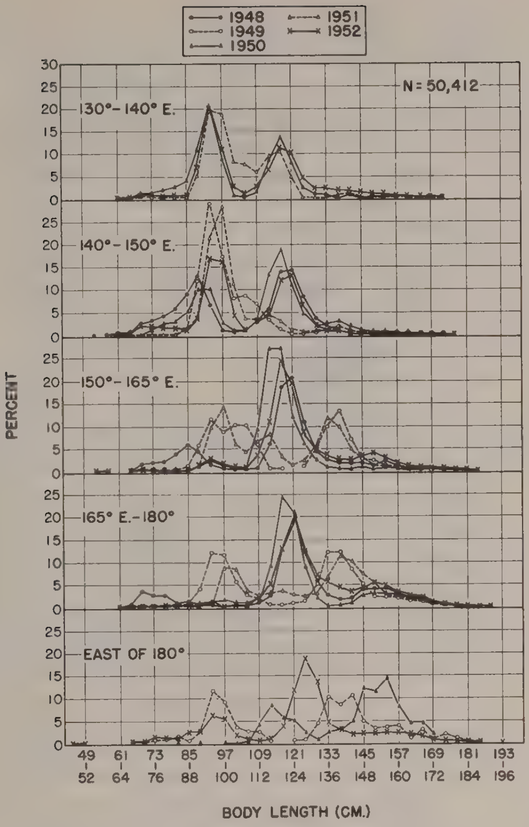

Figure 2.--Length frequencies of bigeye tuna taken in the Japanese North Pacific longline fishery, by longitude of capture. N = total number measured, 1948-52. Based on Kamimura and Honma (1953).

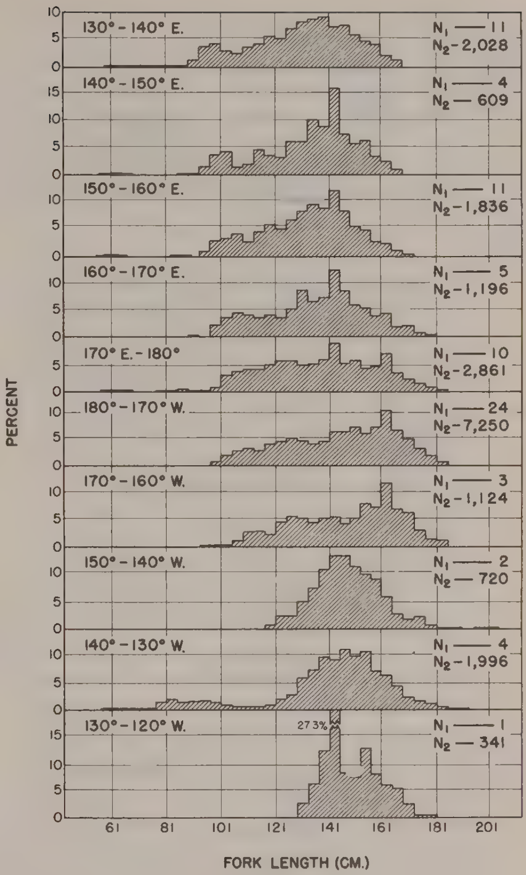

Figure 3.--Length-frequency distribution of bigeye tuna caught by Japanese longlines in 1954, for every 10° of longitude from 130° E. to 120° W. (with the exception of 160°-150° W.) along the 6°-12° N. band. N_1 = number of samples, and N_2 = total number of fish. Adapted from Yukinawa (1958).

Japanese Equatorial Longline Fishery

Yukinawa (1958) reported that bigeye tuna caught during 1954 in the area bounded by lat. 6° to 12° N. and long. 130° E. to 120° W. were 50-200 cm. long; most individuals were between 100 and 160 cm. Modal groups occurred at approximately 100, 120, 140, and 160 cm., the larger sizes being more common toward the east (fig. 3). Moreover, bigeye tuna caught between lat. 6° and 12° N. were slightly larger than those taken south of this area between lat. 2° S. and 6° N. Yukinawa postulated that since the proportion of males was larger in fish above 130 cm. (fig. 4), the higher proportion of large fish north of lat. 6° N. indicated a preponderance of males in this area.

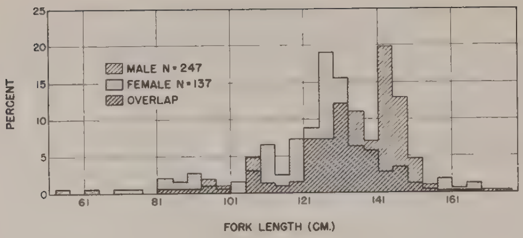

Figure 4.--Length-frequency distribution of male and female bigeye tuna taken in the Japanese equatorial Pacific longline fishery in the area bounded by lat. 2°-9° N. and long. 160°-170° E., July-August 1951. Adapted from Yukinawa (1958).

Exploratory Longline Expeditions to the Equatorial Pacific, 1950-56

Japanese mother ship longline expeditions and exploratory longline cruises by vessels of the U.S. Fish and Wildlife Service, through its Pacific Oceanic Fishery Investigations (POFI)[1], during the early 1950's stimulated the publication of several papers on the size distribution of the deep-swimming tunas in the equatorial Pacific. Murphy and Shomura (1953b) found that lengths of bigeye tuna taken by longline gear on POFI cruises during January-June 1952 ranged from 107 to 197 cm. The larger fish were more plentiful toward the east; i.e., the mean length increased from 134.5 cm. at long. 155° W. to 155.5 cm. at long. 120° W. Shomura and Murphy (1955) discussed the results of six POFI cruises made during 1953 between lat. 15° N. and 15° S., long. 140° and 170° W. in the vicinity of the Line and Phoenix Islands. The bigeye tuna were large (77-182 cm.); about 90 percent of the individuals measured 122-172 cm. (fig. 5).

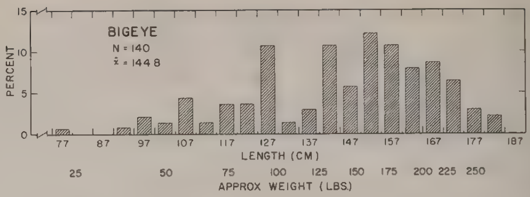

Figure 5.--Sizes of bigeye tuna taken on POFI exploratory longline cruises to the equatorial central Pacific, 1953. N = number measured, x = average length. From Shomura and Murphy (1955).

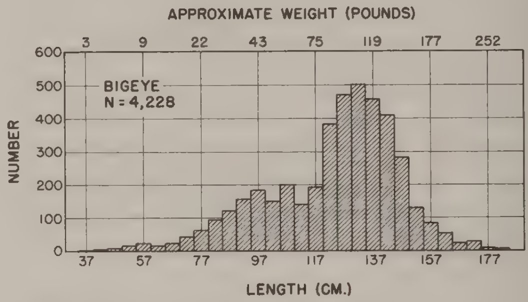

Figure 6.--Size composition of bigeye tuna caught by longline during Japanese mother ship operations in the western equatorial Pacific, June 1950-October 1951. From Murphy and Otsu (1954).

Murphy and Otsu (1954) found that bigeye tuna caught by longline during the nine Japanese mother ship expeditions to the western Pacific (lat. 1° to 10° N.; long. 135° to 179° E.) were 37-182 cm. long; almost 90 percent were between 87 and 152 cm. (fig. 6). These fish seem to be somewhat smaller than those measured by Shomura and Murphy, but if the sex ratios for fish from the two areas were different, any conclusion concerning their relative sizes must be only tentative. Iversen (1955) determined, in fact, that modal lengths of males were about 14 cm. longer than

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[1] Now called the Bureau of Commercial Fisheries Biological Laboratory, Honolulu.

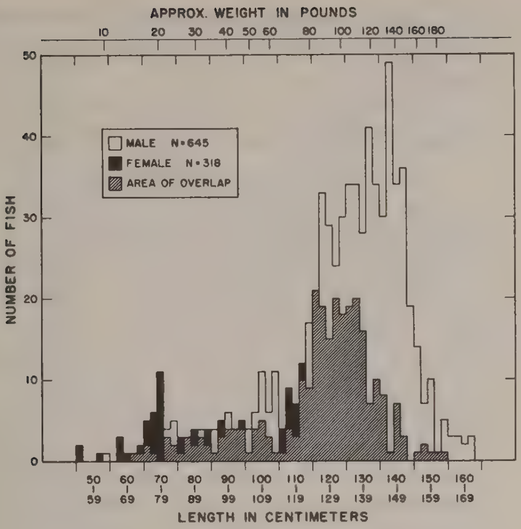

Figure 7.--Sizes of male and female bigeye tuna taken by longline on one Japanese mother ship expedition between long. 137°-165° E., March 29-May 28, 1951. From Iversen(1955).

those for females from a sample of bigeye tuna taken from one of the Japanese mother ship expeditions (fig. 7).

Murphy and Shomura (1955; and unpublished material) have made the most detailed analysis of the size distribution of bigeye tuna across the equatorial Pacific. The length data for fish caught by Japanese and POFI vessels from 1950 to 1954 conform to the theory that the size of bigeye tuna caught on longlines tends to increase from west to east (fig. 8). The average length increased from 122.0 cm. (range 42-162 cm.) in the area farthest to the west (lat. 5° N. to 5° S., long. 138° to 150° E.) to 159.3 cm. (range 112-197 cm.) in the most easterly area (lat. 10° N. to 5° S., long. 122°30' to 117°30' W.). Lengths of bigeye tuna from the

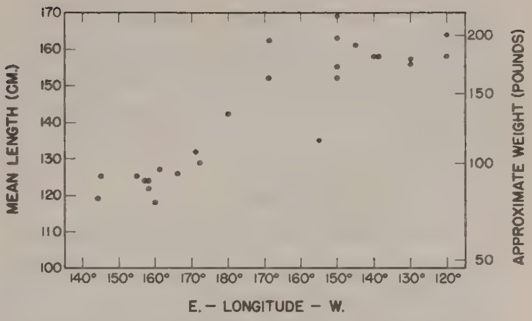

Figure 8.--Mean lengths of samples of bigeye tuna taken by longline plotted against longitude of capture, POFI cruises to the equatorial central Pacific, August-November 1952. From Murphy and Shomura (1955).

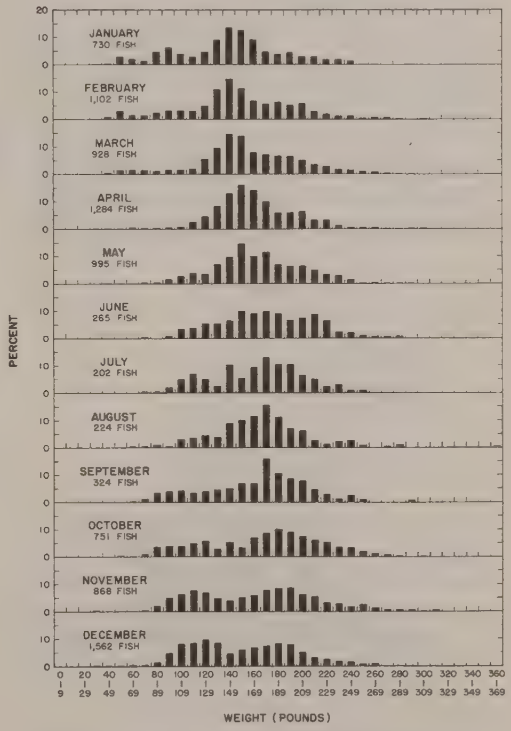

Figure 9.--Monthly percentage weight-frequency distribution of bigeye tuna taken by longline and landed at Honolulu, 1952. From Otsu (1954).

eastern Pacific were obtained from a relatively small number of fish. But it seems likely that the size increase was real and was not due to vagaries of sampling.

Hawaiian Longline Fishery

Otsu (1954) investigated bigeye tuna taken by longline in Hawaiian waters in 1949-52. He presented monthly weight-frequency data for fish landed in Honolulu in 1952, a typical year (fig. 9). Most of the bigeye tuna weighed 100 to 200 pounds; a few fish exceeded 300 pounds. The average weight for the year was about 162 pounds.

Iversen (1955) found that male bigeye tuna landed in 1947-54 outnumbered female; the sex ratio was about 1.5:1.0 in favor of the males. Moreover, modal weights of the males were about 30 pounds heavier than those of the females (fig. 10). Iversen also noticed a persistent difference between adjacent years and a strong resemblance between alternate years in the dominant weight groups.

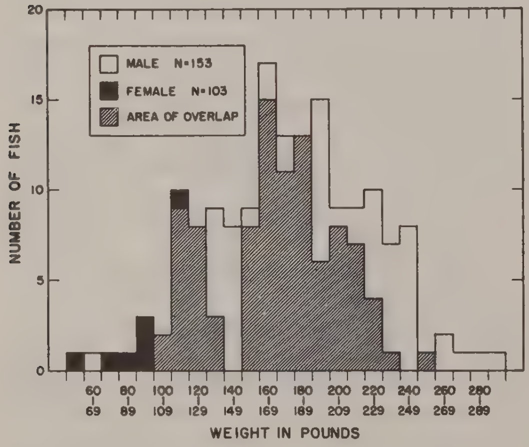

Figure 10.--Weights of male and female bigeye tuna taken by longline and landed at the Honolulu market, May-August 1951. From Iversen (1955).

Japanese Northwest Pacific Live-Bait Fishery

Bigeye tuna taken incidental to the capture of skipjack tuna and albacore during the Japanese spring-summer fishing season are considerably smaller than those taken by longline gear. Honma and Kamimura (1955), who measured bigeye tuna taken during June and July 1953, found two dominant modal groups, one at about 56 cm. and the other at about 76 cm. (fig. 11). The total size range was 42-116 cm. The size distribution by sea area revealed that the bigeye tuna again tended to be smaller in the more westerly areas and were larger, on the average, in more easterly areas.

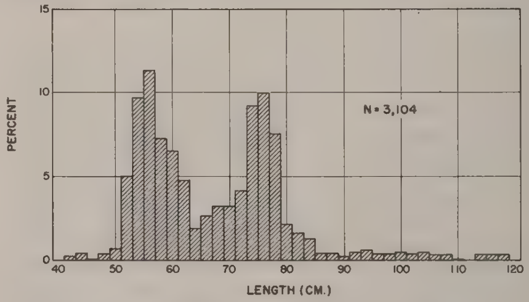

Figure 11.--Length-frequency distribution of bigeye tuna taken by pole and line in the northwestern Pacific, June-July 1953. Based on Honma and Kamimura (1955).

Japanese Longline Fishery in the Eastern Tropical Pacific

Suda and Schaefer (1965a) discussed the recent expansion of the Japanese longline fishery into the eastern tropical Pacific. They estimated that bigeye tuna taken on longlines in 1958-62 weighed an average of 69.5 kg. Barrett and Kume (1965) stated that the range of length for bigeye tuna caught by the longline fishery was 39-209 cm.

U.S. Exploratory Longline Fishing in the Eastern Tropical Pacific

Commercial longline fishing is not practiced by U.S.-based vessels in the eastern tropical Pacific (Alverson and Peterson, 1963). The results of three experimental longline cruises indicate, however, that the deep-swimming bigeye tuna are large. Wilson and Shimada (1955) found that 13 of a total of 14 bigeye tuna caught on an exploratory longline cruise in the area of lat. 13° N. to 3° S., long. 99° to 84° W., were 140-190 cm. long. Most of the bigeye tuna caught on two later exploratory cruises to essentially the same area were not quite so large as those measured by Wilson and Shimada (Mais and Jow, 1960). Nevertheless, the mean length was about 131 cm. (fig. 12).

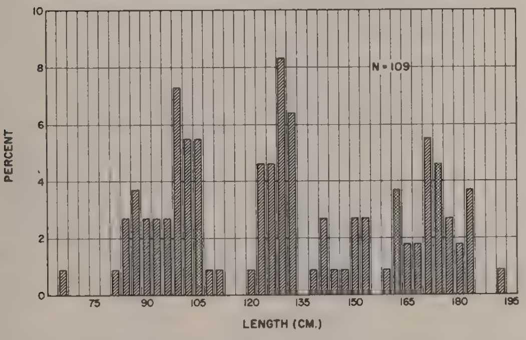

Figure 12.--Lengths of bigeye tuna taken during exploratory longline fishing in the eastern tropical Pacific, 1955-56. Data from Mais and Jow (1960).

Live-Bait Fishery in the Eastern Tropical Pacific

A few bigeye tuna are taken by live-bait fishermen in the eastern Pacific. Alverson and Peterson (1963) reported a size range of 51-199 cm. for fish measured during 1958-61 (fig. 13). Most of these fish were considerably smaller than the deep-swimming bigeye tuna, however, and modal groups were at about 53, 77, and 107 cm. Barrett and Kume (1965) further emphasized this size difference. They pointed out that bigeye tuna shorter than 100 cm. made up more than 50 percent of the catch of the surface fishery in the eastern Pacific in 1955-64, but less than 5 percent of the Japanese longline catch east of long. 130° W. in 1958-64.

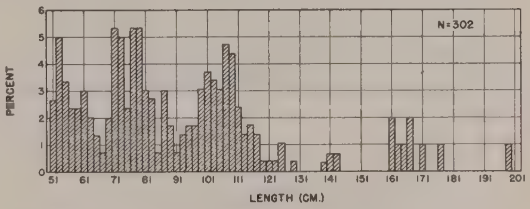

Figure 13.--Length-frequency distribution of bigeye tuna taken by the U.S. live-bait fishery in the eastern tropical Pacific, 1958-61. From Alverson and Peterson (1963).

SIZE DISTRIBUTION OF ALBACORE

Albacore are taken primarily by Japanese longline vessels in their northwestern and South Pacific fishing grounds. A few albacore are also caught by longline around the Hawaiian Islands. Important live-bait fishing areas are the Japanese northwest Pacific spring fishery and the U.S. west coast fishery. Albacore are also exploited commercially in other localities, particularly off Chile and Australia (Yoshida and Otsu, 1963).

Japanese North Pacific Longline Fishery

Nakamura, Kamimura, and Yabuta (1953) found that most albacore taken during 1948-50 were 60-110 cm. long (total range 40-120 cm.). The position of the dominant modes apparently showed an alternate-year cycle, which they attributed to annual differences in growth or recruitment. Additional length-frequency data for 1948-52 illustrate this alternate-year cycle (fig. 14). According to Suda (1954), the two dominant modal groups, 78 and 89 cm., appear alternately in every other year; i.e., the former is dominant in even-numbered years, the latter in odd-numbered years. The total size range was again about 40-120 cm. The lengths attained by the two sexes differed little (fig. 15).

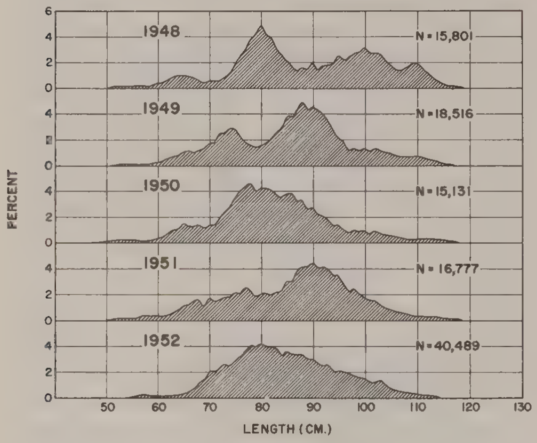

Figure 14.--Length frequencies of albacore caught in the northwestern Pacific during the 1948-52 Japanese longline seasons. Based on Suda (1954).

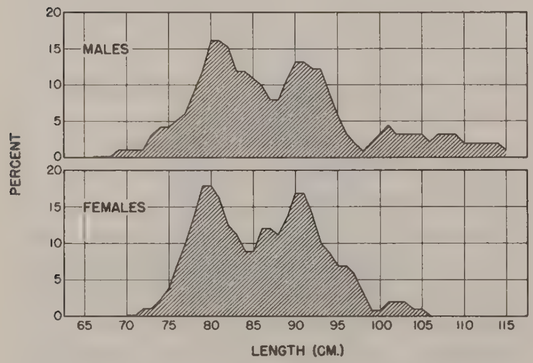

Figure 15.--Lengths of male and female albacore caught in the northwestern Pacific during the 1948-52 Japanese longline seasons. From Suda (1954).

Japanese South Pacific Longline Fishery

Although the albacore evidently has no east-west size gradient, there do seem to be north-south size differences. Albacore taken in the North Equatorial Current and Equatorial Countercurrent areas are considerably larger than those taken to the north. Suda (1956) observed that practically all the fish were longer than 90 cm. during the 1948-53 seasons (fig. 16). But in the South Pacific, Suda (1963) found, at different times, large

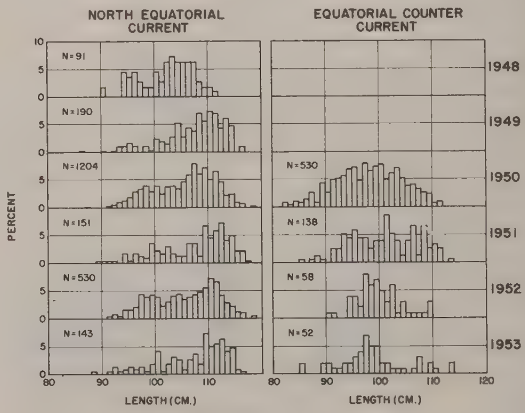

Figure 16.--Lengths of albacore taken on longlines by the Japanese in the North Equatorial Current and Equatorial Countercurrent areas, 1948-53. Based on Suda (1956).

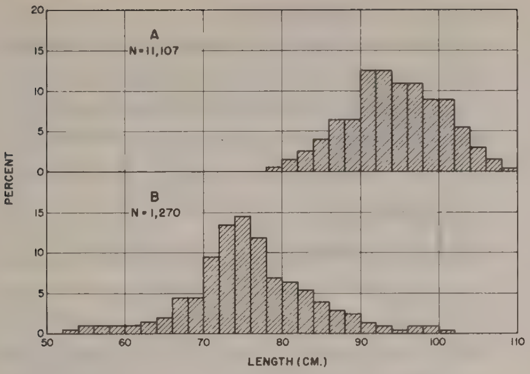

Figure 17.--Length frequencies of albacore in the South Pacific. Panel A includes fish taken by Japanese longlines north of lat. 30° S., December 1952-February 1955. Panel B includes fish taken by Japanese longlines south of lat. 30° S. September-December 1957. Based on Suda (1963).

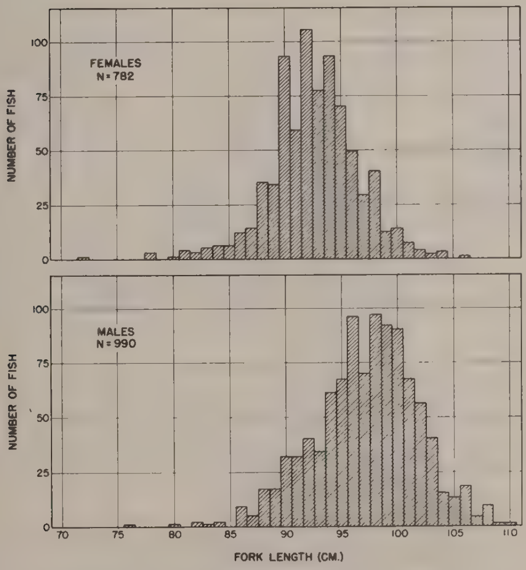

Figure 18.--Lengths of male and female albacore taken by longline and sampled at the tuna cannery in Samoa, August 1957-September 1958. From Otsu and Hansen (1962).

spawning albacore north of lat. 30° S., and small immature fish south of this latitude (fig. 17).

Lengths of albacore landed at American Samoa in 1957-58 ranged from 72 to 110 cm. (Otsu and Hansen, 1962). Males were noticeably larger than females (fig. 18).

Exploratory Longline Expeditions to the Equatorial Pacific, 1950-56

Murphy and Otsu (1954), who reported on the nine Japanese mother ship expeditions to the western Pacific, stated that most of the deep-swimming, longline-caught albacore were 82-112 cm. long (fig. 19). The average length was about 100 cm. All albacore were caught between long. 155° and 179° E. from lat. 1° to 10° N. Large albacore were also taken on POFI exploratory longline cruises south of the Equator from about long. 169° W. to 180° (Murphy and Shomura, 1953b). Almost 70 percent

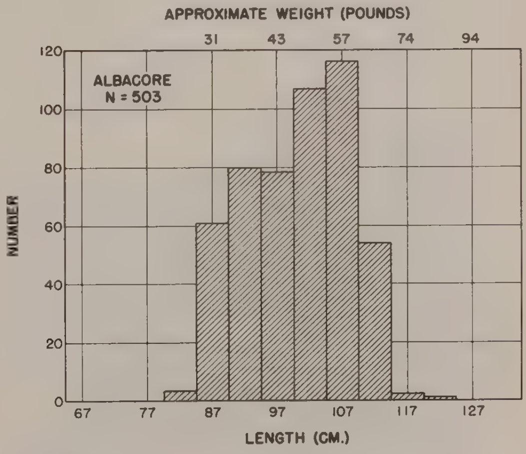

Figure 19.--Size composition of albacore caught by longline during Japanese mother ship operations in the western equatorial Pacific, June 1950-October 1951. From Murphy and Otsu (1954).

(35 of 51) of the fish were between 90 and 100 cm. long. Albacore taken during 1953 were also large; the average weight of 151 specimens was about 40 pounds (Shomura and Murphy, 1955). About 90 percent were 91-103 cm. long (fig. 20).

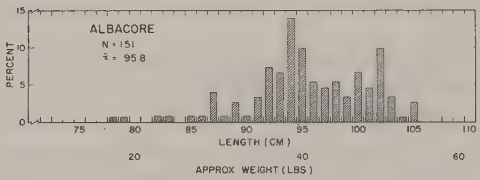

Figure 20.--Length-frequency distribution of albacore taken during POFI longline cruises to the equatorial central Pacific, 1953. N = number measured, $\overline{x}$ = average length. From Shomura and Murphy (1955).

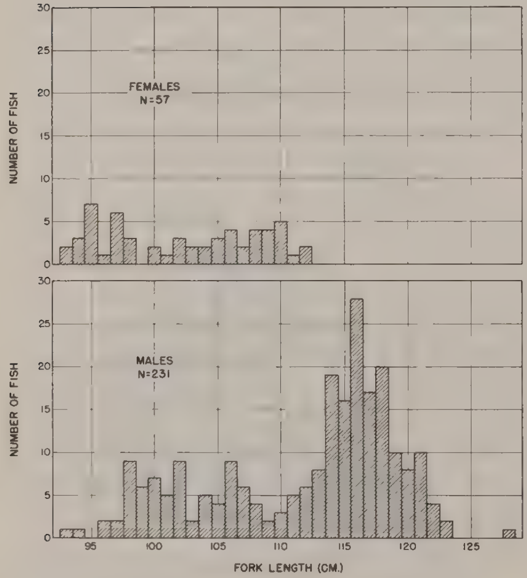

Figure 21.--Lengths of male and female albacore taken in the Hawaiian longline fishery, 1955-56. From Otsu and Hansen (1962).

Hawaiian Longline Fishery

The few albacore taken in Hawaiian waters are mostly very large, mature individuals (Otsu and Hansen, 1962). For example, albacore landed in 1955 and 1956 ranged from 92 to 128 cm. (fig. 21).

Japanese North Pacific Live-Bait Fishery

Albacore taken by pole and line are generally smaller than those taken by longline. For the year 1952, Suda (1963) reported a mean weight of 19.2 pounds for albacore caught by the former method, and 28 pounds for fish taken with longline gear. Uno (1936) found that albacore landed in May and June of 1935 were of small to medium size--approximately 70-90 cm. long (fig. 22).

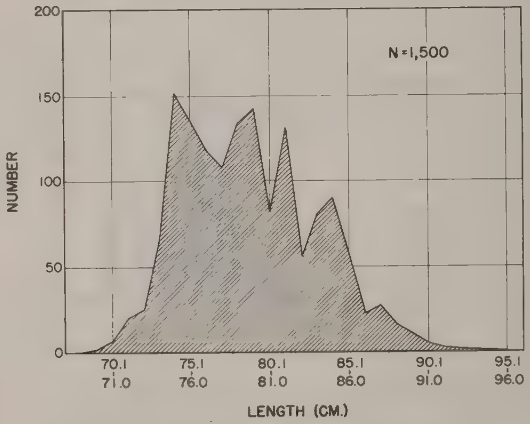

Figure 22.--Length composition of albacore caught by pole and line in Japanese waters, May-June 1935, From Uno (1936).

U.S. Eastern Pacific Surface Fishery

Brock (1943) found that albacore caught at the surface off the coasts of California and Oregon had modal lengths between about 60 and 90 cm.; most fish landed at Astoria, Oregon in 1938-40 were 60-80 cm. long. (fig. 23). Brock noticed that males seemed to predominate among fish smaller than 67 cm., but concluded that this circumstance was probably due to errors in determination of sex.

Partlo (1955) also reported small to medium-sized albacore for British Columbia surface catches during the 1949-51 seasons (fig. 24).

SIZE DISTRIBUTION OF YELLOWFIN TUNA

Yellowfin tuna are captured primarily by U.S. and Peruvian live-bait and purse seine vessels operating in the eastern tropical Pacific, and by Japanese longline craft fishing in the central and western Pacific. They are also taken by the Hawaiian longline fishery (Schaefer, Broadhead, and Orange, 1963).

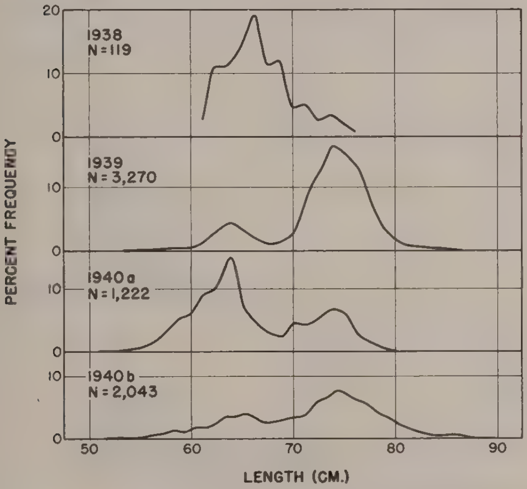

Figure 23.--Length-frequency curves for albacore landed at Astoria, Oregon in 1938-40. Measurements were taken on August 24, 1938, August-October 1939, July 13-21, 1940 (1940a), and July 30-October 14, 1940 (1940b). Adapted from Brock (1943).

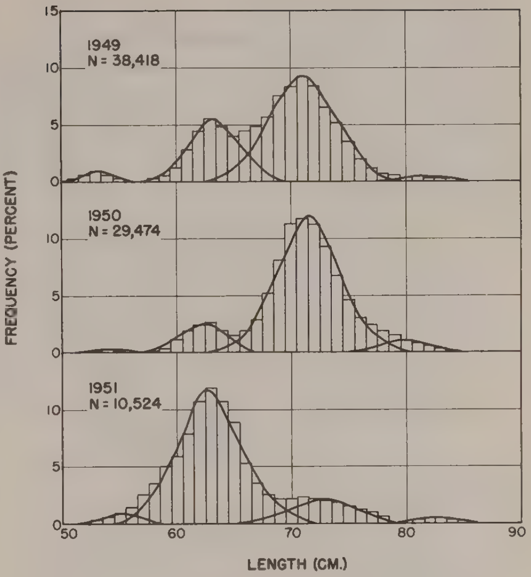

Figure 24.--Comparison of length-frequency distributions of the 1949-51 British Columbia albacore surface catches. Adapted from Partlo (1955).

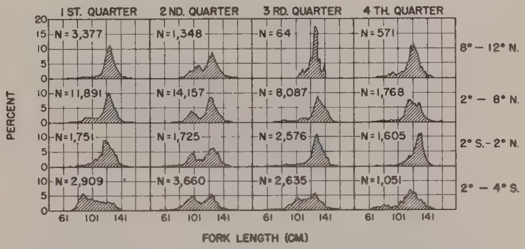

Figure 25.--Length-frequency distributions of yellowfin tuna taken by Japanese longlines between long. 150° and 170° E., at different latitudes, by quarters of the year, October 1952-March 1954. Based on Yukinawa (1958).

Japanese Longline Fishery
Central and Western Equatorial Pacific

Yabuta and Yukinawa (1958) sampled yellowfin tuna caught in waters adjacent to the Eastern Caroline Islands. Length of the fish did not vary greatly from one current system to another between lat. 12° N. to 4° S. and long. 150° to 170° E. (fig. 25). Modal groups appeared at about 90-100 and 120-130 cm. The authors noticed a longitudinal gradient in the size of yellowfin tuna in the equatorial Pacific. For example, the major modal group for fish taken west of 140° E. was 109 cm., whereas that for yellowfin tuna caught in the area 160° to 179° W. was 137 cm. (fig. 26).

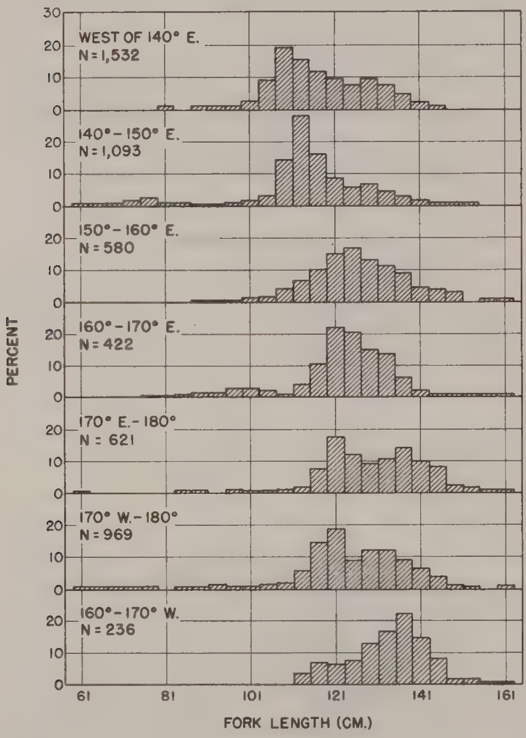

Figure 26.--Length-frequency distributions of yellowfin tuna taken by Japanese longlines, for every 10° of longitude from west of 140° E. to 170° W. between lat. 2° and 8° N. Data for long. 160° to 170° E., and long. 160° to 170° W. were collected from October 1953 to March 1953. Based on Yabuta and Yukinawa (1958).

Exploratory Longline Expeditions to the Equatorial Pacific, 1950-56

Many general principles are well illustrated in the several published reports that deal primarily with the size distributions of yellowfin tuna taken on the Japanese mother ship expeditions and POFI cruises. Shomura and Murphy (1955) discovered that fish from the open sea were slightly larger, on the average, than those caught within 80 miles of land (fig. 27). Although the range of lengths was nearly identical for all fish, and the dominant modal length was 142 cm. in both situations,

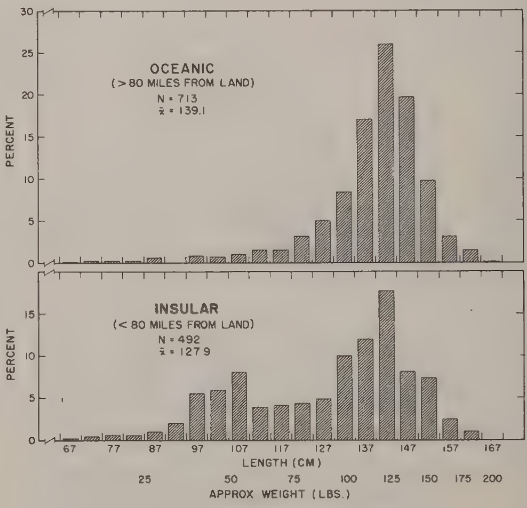

Figure 27.--Lengths of yellowfin tuna from oceanic and insular waters, POFI longline cruises to the equatorial central Pacific, 1953. N = number measured, $\overline{x}$ = average length. From Shomura and Murphy (1955).

yellowfin tuna smaller than 100 cm. were more common closer to land. Iversen and Yoshida (1957) noticed on later cruises that even though the catch rate was generally higher near shore, the insular longline catch (made up of yellowfin tuna taken within 5 miles of land) was composed of slightly smaller individuals than was the oceanic longline catch.

Shomura and Murphy (1955) found that males outnumbered females and attained a larger average size (fig. 28). The sexes were almost equally represented in 1953 for fish taken in the western, central, and eastern equatorial Pacific up to 137 cm. long, but males were much more abundant above this size.

As was true for bigeye tuna and albacore, Murphy and Shomura (1955, and unpublished material) demonstrated that the size of longline-caught yellowfin tuna increases from west to east in the equatorial Pacific (fig. 29). The average

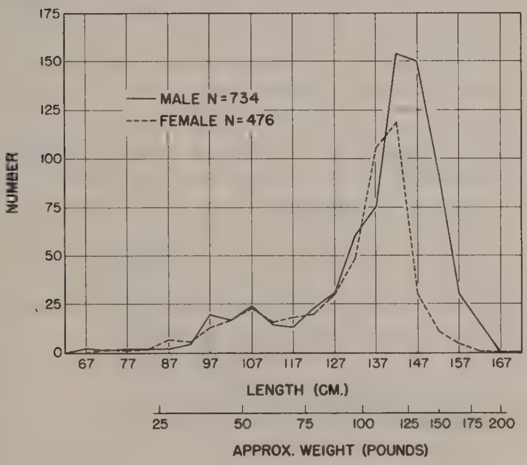

Figure 28.--Length frequencies of male and female yellowfin tuna, POFI longline cruises to the equatorial central Pacific, 1953. From Shomura and Murphy (1955).

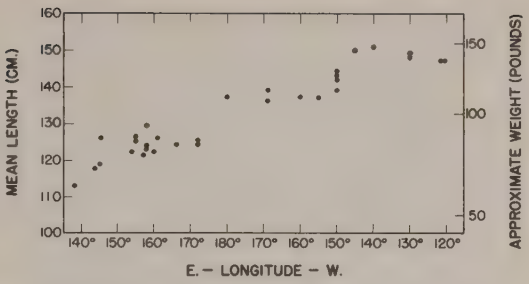

Figure 29.--Mean lengths of samples of longline-caught yellowfin tuna plotted against longitude of capture, POFI cruises to the equatorial central Pacific, August-November 1952. From Murphy and Shomura (1955).

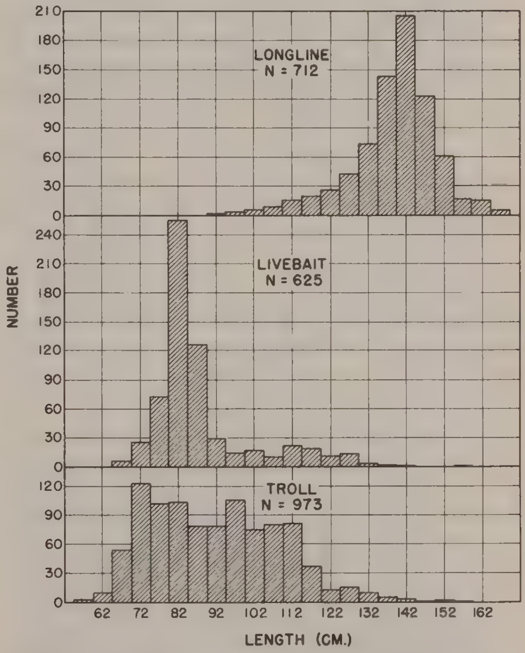

Figure 30.--Lengths of yellowfin tuna taken by various experimental gear. Most fish caught by trolling and live bait were taken near islands in the central Pacific Ocean. Longline-caught fish were taken in deep water during POFI cruises, 1950-51. From Murphy and Shomura (1953a).

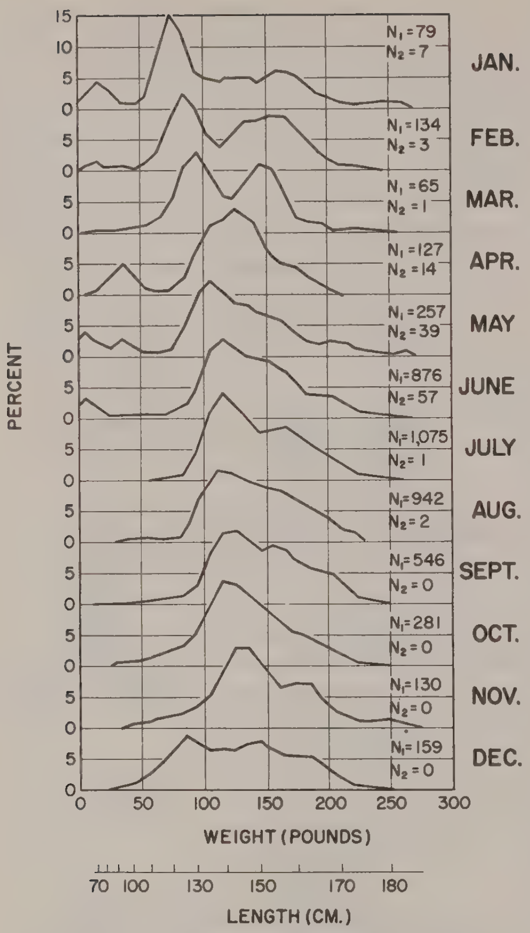

Figure 31.--Weight-frequency distributions of catches of yellowfin tuna landed at Honolulu, 1948-49. Most fish were caught on longlines (N_1), but a few taken by pole and line (N_2) are included for some months. All fish in the latter group weighed less than 40 pounds. Based on Moore (1951).

length increased from 113.1 cm. (range 62-147 cm.) in the area farthest to the west (long. 134° to 141° E.) to 142.5 cm. (range 42-167 cm.) in the most easterly area (long. 122°30' to 117°30' W.).

Murphy and Shomura (1953a) pointed out that sizes of yellowfin tuna caught by live bait, trolling, and longline were different (fig. 30). Whereas the major portion of the central Pacific longline catch was composed of fish 132-152 cm. long, most yellowfin tuna taken near islands by pole and line and by trolling were 77-92 and 67-117 cm., respectively. Iversen and Yoshida (1957) also noticed a difference in size between yellowfin tuna caught by trolling and those taken by longlining. The size range was about the same for fish in the two groups (50-151 cm. for troll-caught, and 47-163 cm. for longline-caught fish). But the dominant length group was 140-149 cm. for deep-swimming yellowfin tuna taken on longline gear, as compared with 70-79 cm. for the surface-swimming fish caught by trolling.

Hawaiian Fishery

Moore (1951) plotted monthly weight-frequency distributions for yellowfin tuna caught in 1948-49 (fig. 31). Most of the few fish taken by live-bait fishing and trolling weighed less than 10 pounds; the heaviest fish were in the 30- to 39-pound size class. On the other hand, 90 percent of the longline-caught yellowfin tuna weighed 90-219 pounds (range, 20-269 pounds). Yellowfin tuna taken on longlines in 1947-56 were reported to weigh, on the average, about 140 pounds (Otsu, 1954; Shomura, 1959).

U.S. Eastern Tropical Pacific Live-Bait and Purse Seine Fishery

Wilson and Shimada (1955) sampled the catch of one tuna clipper operating off the coast of Central America in February 1953. The yellowfin tuna caught by pole and line were small. Almost 90 percent were 45-80 cm.

long (fig. 32). Hennemuth (1961) found a greater size range (about 40-160 cm.), and most of the fish were 50-100 cm. long (fig. 33). Schaefer, Broadhead, and Orange (1963) stated that yellowfin tuna taken by live bait and purse seines in the eastern Pacific weigh between 7.5 and 200 pounds. Fish of 10-40 pounds dominate the live-bait catch, but according to Hennemuth (1961) those taken by purse seining are somewhat larger. For 1964, the preliminary estimate of the mean weight of yellowfin tuna caught by both methods was 23.6 pounds, an increase of 3.4 pounds over 1963 (Inter-American Tropical Tuna Commission, 1965).

Some evidence suggests that size differences of yellowfin tuna from one sample to another may be attributable to a tendency for fish of similar size to school together, much as Schaefer (1948) had previously suggested. Broadhead and Orange (1960) who sampled bait-boat catches, found that yellowfin tuna from pure schools were 50 to 110 cm.

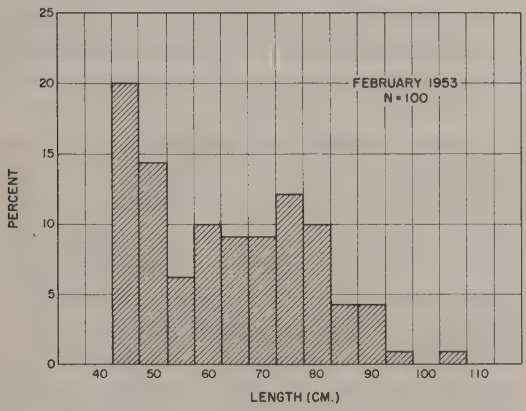

Figure 32.--Length-frequency distribution of yellowfin tuna caught by live-bait fishing in the eastern tropical Pacific, February 1953. Data from Wilson and Shimada (1955).

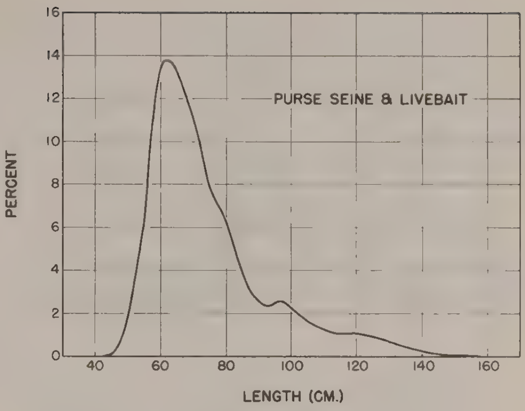

Figure 33.--Length-frequency distribution of yellowfin tuna taken by live-bait and purse seine fishing in the eastern tropical Pacific, 1954-58. From Brock (1962), based on data from Hennemuth (1961).

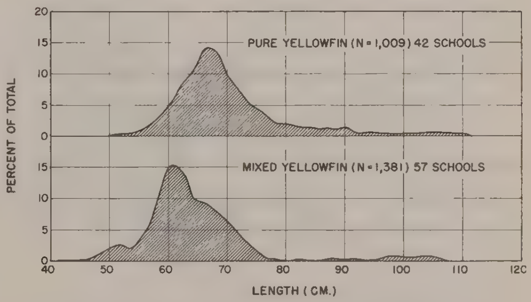

Figure 34.--Comparison of length-frequency distributions of yellowfin tuna from pure schools and mixed-species schools, as sampled from bait boat catches in the eastern Pacific, 1956-58. "Mixed yellowfin" refers to yellowfin tuna in association with small skipjack tuna (see figs. 45 and 46). Adapted from Broadhead and Orange (1960).

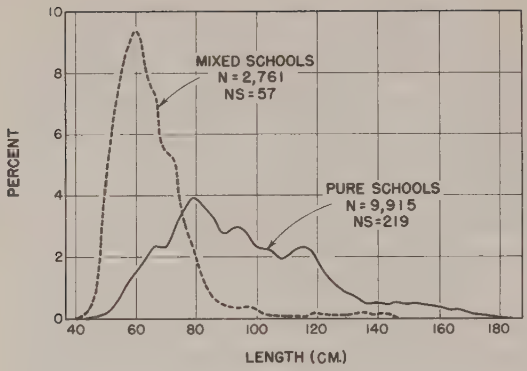

Figure 35.--Comparison of lengths of yellowfin tuna from pure schools and mixed schools (associated with skipjack tuna), as sampled from purse seine catches in the eastern Pacific. N = number of yellowfin tuna measured, NS = number of schools fished. Adapted from Calkins (1965).

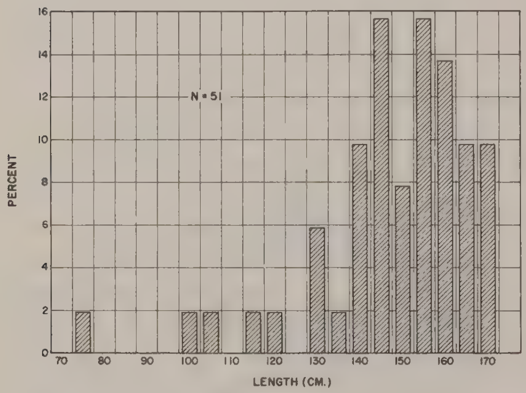

Figure 36.--Length-frequency distribution of yellowfin tuna taken by longline, January-March 1953, in the eastern tropical Pacific. Data from Wilson and Shimada (1955).

long and had a distinct mode at about 65-69 cm. (fig. 34, upper panel). On the other hand, yellowfin tuna from mixed schools tended to approximate more closely the smaller size of the skipjack tuna with which they were associated. The dominant length group for the latter group of yellowfin tuna was at about 59-63 cm., and the range included fish from 41 to 107 cm. (fig. 34, lower panel). Calkins (1965) found that yellowfin tuna taken by purse seining from pure schools were commonly longer than 70 cm., although a much greater size variation was noticed than for yellowfin tuna from mixed schools (fig. 35). The dominant modal length of the yellowfin tuna which were associated with skipjack tuna was again about 60 cm.

Exploratory Longline Expeditions to the Eastern Tropical Pacific

The results of three exploratory longline cruises to the eastern tropical Pacific were described by Wilson and Shimada (1955) and Mais and Jow (1960). Yellowfin tuna taken on the first cruise were considerably larger than those usually taken by surface fishing, and fully 90 percent of the individuals were 130 to 170 cm. long (fig. 36). The mean length was about 147 cm. The majority of the yellowfin tuna taken on the two later cruises were somewhat smaller, measuring 90-110 cm. (fig. 37).

Japanese Longline Fishery in the Eastern Tropical Pacific

Suda and Schaefer (1965b) recently analyzed length composition data for yellowfin tuna caught by Japanese longline vessels east of long. 130° W. in 1958-62. For the entire area, yellowfin tuna 130 to 150 cm. long make up about one-half the total yearly catch. During the winter, small fish with a mode near 125 cm. are most plentiful; these fish then grow to about 138 cm. to dominate the summer catch. The proportion of large fish tends to increase from west to east. The authors speculate that the size gradient is due to a difference in the availability of the larger, deeper-swimming yellowfin tuna to the longline hooks. Finally, males are more numerous than females, particularly among fish longer than 150 cm. Above this length, 75 percent are males; and males make up 91 percent of all bigeye tuna longer than 160 cm.

SIZE DISTRIBUTION OF SKIPJACK TUNA

Most skipjack tuna are caught by Japanese fishermen by live-bait and purse seine methods in the northwestern Pacific, and by U.S. and Peruvian fishermen in the eastern Pacific. Skipjack tuna are also taken commercially around the Hawaiian and Palau Islands, and on a subsistence basis in many other locations in Micronesia, Melanesia, and Polynesia (Waldron, 1963).

Japanese Northwestern Pacific Fishery

Kawasaki (1955) contended that slight differences in the lengths of skipjack tuna depended on whether the fish were "shoal-associated" or "migratory." The stationary group consisted of fish with modal lengths of 40-50 and 60-70 cm. The group which migrated along current boundaries had modes at 30-40 and 50-60 cm. (fig. 38).

Exploratory Longline Expeditions to the Equatorial Pacific, 1950-56

Murphy and Shomura (1953b) reported that 17 skipjack tuna were caught during POFI cruises to the equatorial Pacific, January-June 1952. Fifteen of these fish were 76-82 cm. long, and the range was 66-82 cm. A few more skipjack tuna were taken on similar expeditions in 1953 (Shomura and Murphy, 1955).

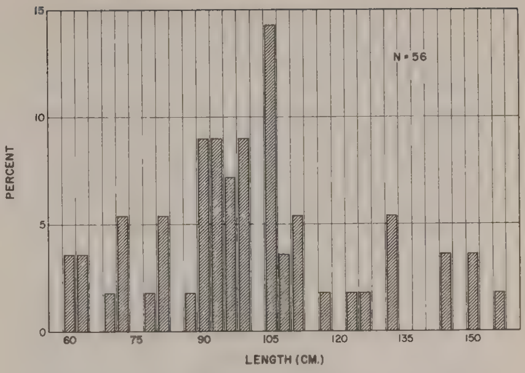

Figure 37.--Length-frequency distribution of yellowfin tuna taken by longline in the eastern tropical Pacific, September-November 1955 and January-March 1956. Data from Mais and Jow (1960).

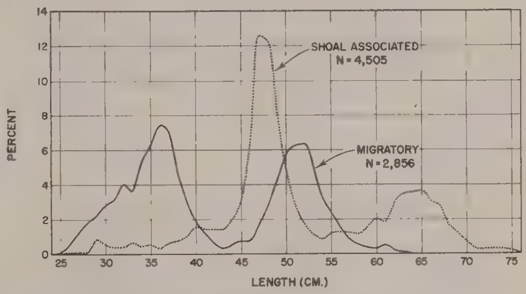

Figure 38.--Length-frequency distributions of "shoal-associated" and "migratory" skipjack tuna in the southwestern sea area of Japan, July-October 1954. Based on Kawasaki (1955).

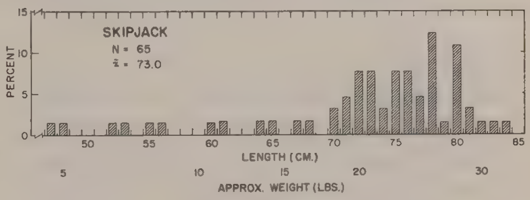

Figure 39.--Size-frequency distribution of skipjack tuna taken during POFI longline cruises to the equatorial central Pacific, 1953. N = number measured, $\overline{x}$ = average length. From Shomura and Murphy (1955).

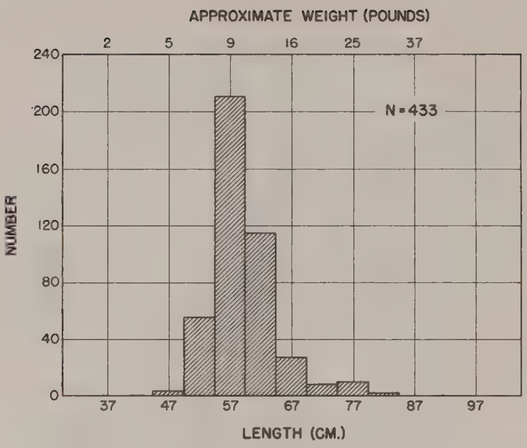

Figure 40.--Size composition of skipjack tuna caught by longline gear during Japanese mother ship expeditions to the western equatorial Pacific, June 1950-October 1951. From Murphy and Otsu (1954).

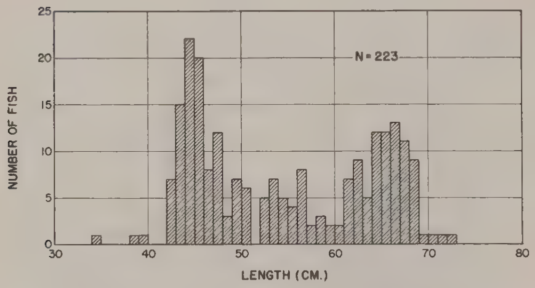

Figure 41.--Lengths of skipjack tuna taken by trolling near the northern Marshall Islands, April-August 1946 and July-August 1947. From Marr (1948).

These fish were large. Their lengths ranged from 47 to 84 cm., and 90 percent of the catch fell between 70 and 81 cm. (fig. 39). All skipjack tuna were taken in the area bounded by lat. 9° N. to 6° S. and long. 140° to 170° W.

Skipjack tuna were also taken in small numbers during the nine Japanese mother ship expeditions to the western equatorial Pacific from June 1950 to October 1951 (Murphy and Otsu, 1954). The average length of 59 cm. for fish caught in this area (lat. 24° N. to Equator, long. 130° to 179° E.) was smaller than that Murphy and Shomura reported for skipjack tuna to the east, although the range of lengths (47-82 cm.) was practically the same (fig. 40). Most skipjack tuna were between 53 and 63 cm. long.

Exploratory Fishing Near the Northern Marshall Islands

Marr (1948) measured 223 skipjack tuna taken on trolling lines near the northern Marshall Islands in spring and summer, 1946-47. The bulk of the fish were 40-70 cm. long (fig. 41).

Western Equatorial Live-Bait Fishing Near the Palau Islands

Only preliminary information is available for skipjack tuna caught by bait boats near the Palau Islands from June to December 1965. These fish seem to be smaller than the ''season fish'' taken around the Hawaiian Islands during the summer. The major modal group for June falls at 51 cm., whereas that for October is at 59 cm. (fig. 42). Minor peaks in the two frequency distributions occur at 43 and 50 cm., respectively. The total ranges for skipjack tuna were 31-63 cm. for June and 45-73 cm. for October.

Hawaiian Live-Bait Fishery

Brock (1954) grouped length measurements by 6-month periods for skipjack tuna caught in 1946-51 (fig. 43). The length-frequency curves are bimodal or trimodal, with fish centered around lengths of 45, 70, and 80 cm. The 70-cm. group formed the bulk of the catch.

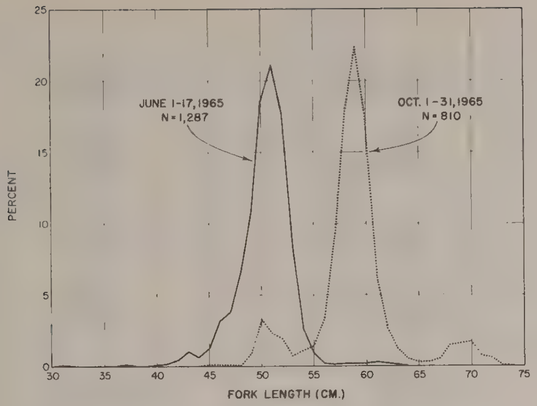

Figure 42.--Preliminary length-frequency distributions for skipjack tuna caught in the bait fishery around the Palau Islands, June 1-17 and October 1-31, 1965.

Rothschild (1965) presented monthly length-frequency data for 1952-63 (fig. 44). These distributions indicate that modal lengths of about 35, 50, and 70 cm. are common during the winter, whereas skipjack tuna landed during the summer are typically about 45 and 70 cm. long. Fish larger than 60 cm. invariably make up over 50 percent of the total catch during at least one of the summer months.

U.S. Eastern Tropical Pacific Live-Bait Fishery

Catches of skipjack tuna by pole and line off the west coast of the Americas are usually dominated by fish which are 50 to 60 cm. long (fig. 45), and have a range from about 40 to 70 cm. (Broadhead and Orange, 1960). Broadhead and Barrett (1964) emphasized, however, that skipjack tuna larger than 60 cm. may occasionally be common in some areas. Many of the skipjack tuna caught by pole and line near the Revillagigedo Islands during the excellent fishing years of 1955 and 1956 (fig. 46) were, in fact, of a size similar to that common in the Hawaiian fishery.

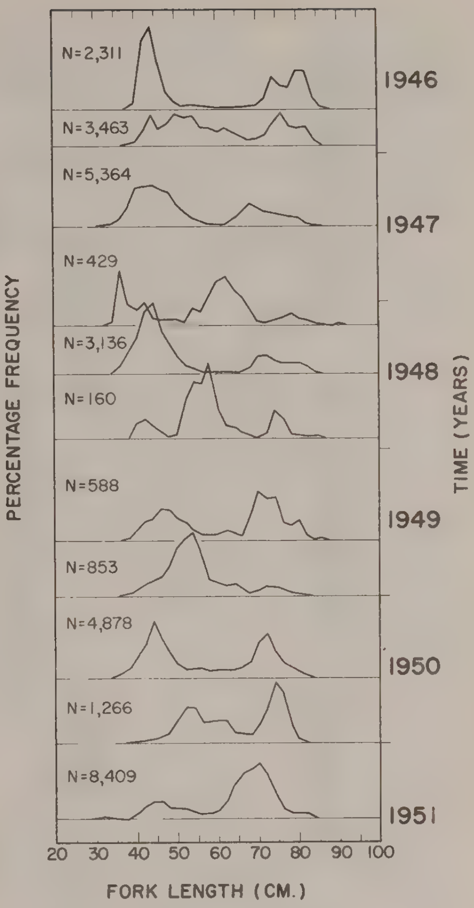

Figure 43.--Length frequencies of Hawaiian skipjack tuna, grouped by time periods of approximately 6 months, 1946-51. Adapted from Brock (1954).

DISCUSSION

The size distributions of the four species of tuna described in this paper permit several generalizations. For example, it is clear from the size-

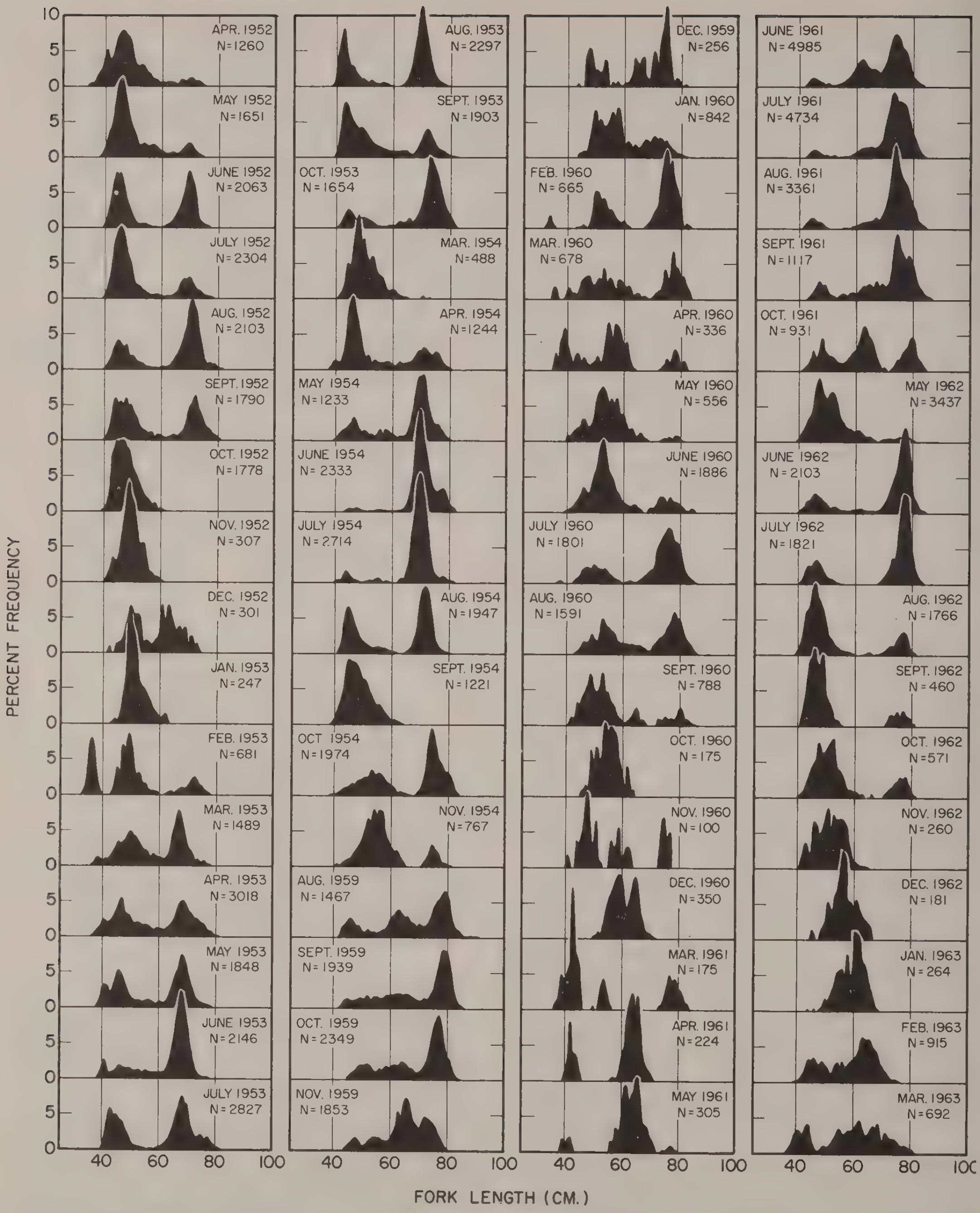

Figure 44.--Monthly length-frequency distributions of skipjack tuna caught by the Hawaiian fishery, 1952-54 and 1959-63. From Rothschild (1965).

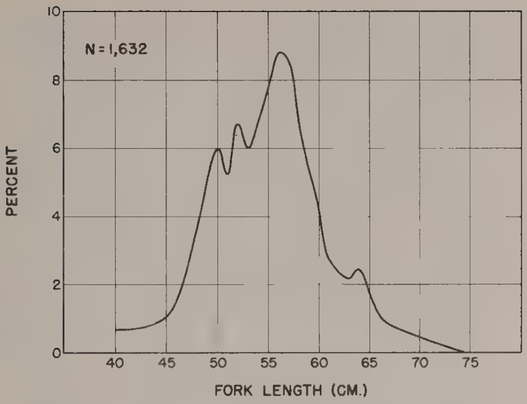

Figure 45.--Length-frequency distribution of skipjack tuna taken by bait boats in the eastern Pacific in 1956-58, areas of catch not specified. From Broadhead and Orange (1960).

frequency data presented in figures 1-46 that fundamental differences exist in the sizes of tuna caught in different areas of the Pacific. The consensus of several workers is that the average size of bigeye and yellowfin tunas captured by longline increases from west to east across the equatorial Pacific (Murphy and Shomura, 1953a, 1953b, 1955, and unpublished data; Shomura and Murphy, 1955; Murphy and Otsu, 1954; Iversen and Yoshida, 1956, 1957; Yukinawa, 1958; Yabuta and Yukinawa, 1958; Suda and Schaefer, 1965b). The same generalization holds true for the North Pacific, where large bigeye tuna tend to predominate to the east and small fish to the west (Kamimura and Honma, 1953). Furthermore, larger skipjack tuna and albacore are usually caught around the Hawaiian Islands than in the eastern Pacific or near Japan (Rothschild, 1965; Broadhead and Barrett, 1964; Yoshida and Otsu, 1963). In the South Pacific the albacore that occur closer to the Equator tend to be larger than those from southern temperate waters (Suda, 1956, 1963).

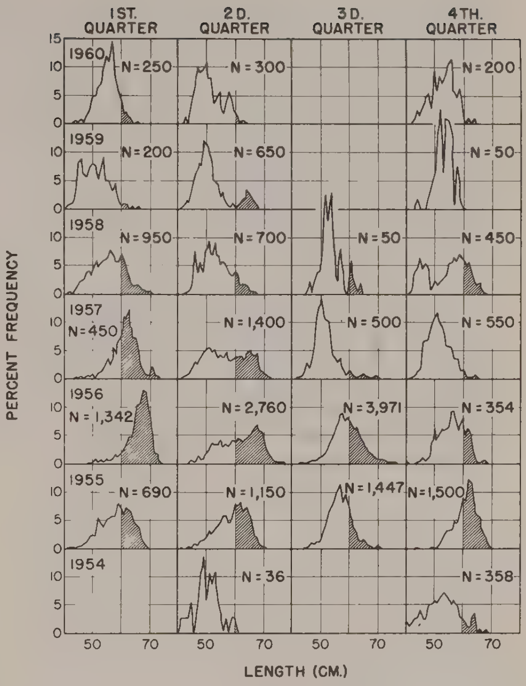

Figure 46.--Length frequencies of skipjack tuna caught by pole and line, by quarter of the year, for the Revillagigedo Islands area, 1954-60. Cross-hatched portions of curves represent fish longer than 60 cm. From Broadhead and Barrett (1964).

Periodic or seasonal variations in the sizes of tuna are common to all fishing areas in the Pacific. Inter-year and intra-year fluctuations in the dominant modal size-classes have been discussed in terms of differences in recruitment, growth rate, and migration for the bigeye tuna (Nakamura, Kamimura, and Yabuta, 1953; Kamimura and Honma, 1953), the yellowfin tuna (Iversen, 1955, 1956; Suda and Schaefer, 1965b), and the albacore (Nakamura, Kamimura, and Yabuta, 1953; Suda, 1954, 1956). In the resulting complex situation, dominant modal groups may progress or regress with time owing to growth of successive year classes, migrations into or out of the fishery area, fluctuations in mortality and recruitment, or a combination of these and other events. In a population that exists in a closed system, growth of year-classes should produce a progression of modal size-classes with time, whether or not each major mode represents a different age group. If modes do not progress, but appear to remain stationary or regress, as Iversen (1956) found to be true for equatorial yellowfin tuna, then other factors must be compensating for growth.

Many workers have emphasized that tunas may undertake extensive migrations at certain stages of their life. Individual adolescent skipjack tuna may migrate from a westward area such as Hawaii and contribute larger fish to the eastern Pacific fishery (Broadhead and Barrett, 1964). Recently, on the basis of length-frequency data, as well as other information available from tagging experiments, immunogenetic affinities of subpopulations, and distribution of immature stages, Kawasaki (1964) and Rothschild (1965) have advanced sets of hypotheses concerning the intimate interrelationships of the skipjack tuna in all parts of the North Pacific. The fundamental differences in the size frequencies of tunas in the different areas could be ascribable to these migrations, the complex nature and causation of which have yet to be elucidated.

The size of some tunas may also vary according to their proximity to land. Yellowfin tuna caught near islands tend to be smaller, on the average, than those taken in the open sea (Shomura and Murphy, 1955; Iversen and Yoshida, 1957). Similarly, shoal-associated skipjack tuna are generally smaller than offshore fish, at least in the southwestern sea area of Japan (Kawasaki, 1955).

The several types of fishing gear and fishing methods tend to catch tuna of different sizes. Longlines capture more large and fewer small fish than do the types of gear that fish at lesser depths. Among the surface-fishing methods, purse seines tend to catch slightly larger tuna than do live-bait or trolling techniques. Indeed, it is possible that there is an ecological separation of large and small fish, as well as a greater efficiency of each type of gear at certain depths (Murphy and Otsu, 1954). Several observations also suggest that schooling behavior may play an important role. For example, small skipjack tuna seem to be more strongly inclined than large individuals to form close-knit, relatively permanent schools (Magnuson, 1963). The fact that yellowfin tuna caught on adjacent longline hooks had smaller mean lengths than those caught individually along a longline led Brock (1962) to conclude that large yellowfin tuna occur in smaller schools, and are for this reason more susceptible to capture.

Some variations in the sizes of tunas caught may be due to other aspects of schooling behavior. Yellowfin tuna taken from ''pure schools'' tend to be larger than those associated with skipjack tuna in ''mixed schools'' (Broadhead and Orange, 1960; Calkins, 1965). Yuen (1963) has pointed out, however, that small yellowfin and skipjack tunas may not really form homogeneous aggregations in the sense that they respond to each other and act as a unit. Rather, underwater observations indicate that there is perhaps a response to an external stimulus that brings together tuna of similar size. Yuen hypothesized that this stimulus is food of mutual interest to certain-sized fish of both species.

Finally, males are often distinctly larger, on the average, than females. This disparity becomes particularly significant whenever the expected sex ratio varies from equality. For example, male bigeye tuna are larger and more numerous than females in the equatorial Pacific (Otsu, 1954; Iversen, 1955; Yukinawa, 1958). Yellowfin tuna exhibit similar inequalities in this region (Murphy and Shomura, 1955), as well as in the central and western Pacific (Iversen, 1956) and eastern Pacific (Suda and Schaefer, 1965b). Female Hawaiian skipjack tuna are less abundant than males in the fall season (Brock, 1954). Large males also dominate albacore landings in Hawaii (Otsu and Uchida, 1959) and Samoa (Otsu and Hansen, 1962).

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Effect of Growth Pattern and Exploitation Features on Yields of Pink Salmon in the Northwestern North Pacific

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ABSTRACT

A "rational" scheme of pink salmon exploitation in the Northwestern North Pacific was described recently by T. Doi. The scheme includes a 4-month term of offshore exploitation and inshore harvests of one-half of the resulting return; additionally, an offshore wastage coefficient equal to 0.5 F was assumed and a monomolecular pattern of weight growth during the last 4 months at sea. In this paper, yields are compared under various sets of natural conditions, and conditions of fishing. Yield relations are examined by means of Doi's index of rationality of offshore fishing and an alternative measure (the highest admissible inshore yield under protection of a specified target escapement). Fishery-connected variables include duration of offshore fishing, wastage, and inshore–offshore distribution of effort, given spawner requirements ranging from 17 to 50% of the return when offshore fishing is absent. In terms of effort distribution, unique solutions were obtained which are optimal with respect to total yield and target escapement.

INTRODUCTION

The assessment of offshore yields from salmon populations proceeds frequently from a study of variations in biomass which determine when the weight of the excess over a required spawner reserve is maximal. In a special theoretical case treated by Ricker (1958, p. 33), the instantaneous rates of weight increase and of natural mortality were considered equal so that the biomass, or a fished fraction thereof, may be expected to remain the same regardless of when the fishing is done. When these rates differ, the size of the yield becomes a function of time. For example, recent studies of sockeye salmon by Ricker (1962) and Fredin (1964) indicated higher oceanic rates of growth than of natural mortality and led to the conclusion that yields attainable offshore would be lower than those attainable inshore provided either fishery is capable of taking a percentage of the run such that a desired number of salmon survive to spawn. It follows that, under the same spawner requirement, a combination of offshore and inshore fishing would produce yields that are intermediate between those achievable inshore alone, or offshore alone. Such combined yields are simply and conveniently expressed as fractions of weight attained by the harvestable excess.

The rationality of combined inshore and offshore exploitation of stocks of pink salmon in the Northwestern North Pacific was the subject of a recent study by Doi (1962) in which the assessment of yield proceeded along different lines. Common to all combinations considered by him was the restriction of inshore exploitation rate to a single value which, in the absence of offshore fishing, would result in a higher spawner level than the level which now survives joint exploitation and is considered acceptable in regard to the reproductive requirements of these stocks. In the graphs presented by Doi, inshore exploitation rate is implicit; the variables treated explicitly are those commonly displayed in isopleths of marine fisheries (i.e., instantaneous rate of fishing mortality and age at first capture). In the present paper similar emphasis is placed on both components of effort by treating inshore as well as offshore fishing mortality rates explicitly.

Doi's comparisons of yield are made in terms of index values, which are critically affected by the duality in spawner level mentioned. The base of the index is an inshore yield chosen to account for but a part of the harvestable excess, whereas optimality of the combined yields so indexed is made contingent upon complete removal of the excess. Thus, inequality of escapement is a precondition of Doi's method of assessment, whereas the assessments of Ricker (1964) presuppose equality in this respect. For practical purposes, the inequality restricts Doi's search for optimal combinations of effort to situations in which the inshore fishery is incapable of taking the harvestable excess in the event that prior offshore fishing has been absent.

The index values in Doi's paper are easily rescaled to express yield in terms of harvestable excess, and the range of his comparisons can be expanded to include all combinations of effort that will leave a given target escapement intact. The demonstration of yield optimality under these conditions is the main purpose of the present paper. It begins with a display of three patterns of offshore growth in weight which include, or are based on, the growth function supplied by Doi (1962). It is then shown how these patterns affect the development of maximum biomass in time, how offshore yields are affected by extending the period of exploitation from 1 to 4 months and, in the latter case, by wastage (i.e., the fatal interception of fish without capture). Comparisons of combined yields are made next, first in Doi's terms, then by indices in which his restrictions are removed by steps, and finally replaced by a single restriction based on target escapement. One of Doi's isopleths is reconstructed after correcting for underestimates in offshore yield. Other isopleths are based on the rate of natural mortality from which his present conclusions regarding optimal schemes of exploitation are inferred. Finally, the effects of different regimes of exploitation are shown when the rates of growth and natural mortality are similar to those found for North American stocks of pink salmon.

PARAMETERS AND EQUATIONS

Some symbols used by Doi (1962) are retained here to facilitate comparison but others have been changed or added for convenience in discussion.

t—Ocean age in months counted from the beginning of the fourth month before return to inshore waters

$t_{\rho'}$—Age at first exploitation (months); $0 \leqslant t_{\rho'} \leqslant 4$

t_c—Age at coastal return; $t_c \equiv 4$ months

τ—Duration of offshore fishing (months); $\tau = t - t_{\rho'}$, $t \geqslant t_{\rho'}$

N_t—Number of fish alive at time t; $N_0 = 1{,}000$

P—Number of fish surviving to spawn

Y—Yield per 1,000 recruits, in kilograms

M—Instantaneous rate of mortality due to natural causes (per month)

$(1+k)F$—Instantaneous rate of mortality due to fishing (per month)

k—Coefficient of wastage

E—Exploitation rate

$w_1(t) = 1.00 \exp(0.1419t)$

$w_2(t) = 1.00 + 0.191t$

$w_3(t) = 2.04 - 1.04 \exp(-0.332t)$; cf. equation (6) in Doi (1962)

$B(i)$—Mean biomass over the interval of exploitation, expressed as function of the set $i = \{w(t), M, F_o', k, t_{\rho'}\}$

o, c—Letter subscripts referring to ocean or coastal parameters, or variables

$'$—Prime, implying that a run is exploited both offshore and inshore. For example, Y_c' is the coastal, or inshore yield of survivors from offshore fishing. When the choice of a parameter is contingent on joint exploitation, it is termed "conditional."

I—Index of rationality of offshore fishing, cf. expression (7)

Absolute offshore yield (Y_o) is obtained from the general relation

$$dY_o = F_o(t)N(t)w(t)dt \qquad (1)$$

and evaluated from

$$Y_o \doteq \tau F_o N_{t_{\rho'}} w_{t_{\rho'}} \int_0^1 w(t) e^{-\tau[M+(1+k)F_o]\tau_1} d\tau_1 \qquad (2)$$

where τ_1 enters as variable of integration, and τ as defined. The growth functions $w(t)$ as written earlier were used to evaluate individual fish weight at the beginning of the offshore fishing term ($w_{t_{\rho'}}$); for use in integrating they are rewritten as follows to conform to the lower limit of integration:

$$w_1(t) \rightarrow w_{t_{\rho'}} e^{0.1419\tau}, \qquad (3)$$

$$w_2(t) \rightarrow w_{t_{\rho'}}(1.00 + 0.191\tau), \qquad (4)$$

$$w_3(t) \rightarrow 2.04 - (2.04 - w_{t_{\rho'}}) e^{-0.332\tau}. \qquad (5)$$

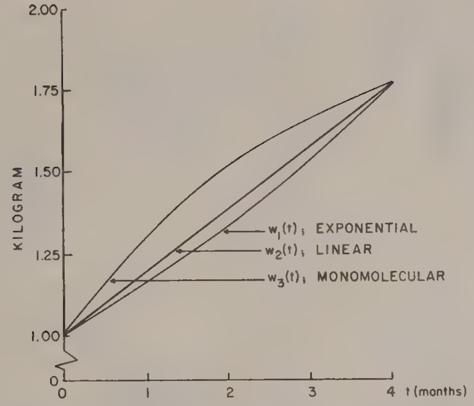

Figure 1.—Far Eastern pink salmon growth in weight during the last 4 months of ocean residence, under three assumptions regarding growth pattern (based on Doi, 1962).

Doi's formula (6) is equivalent to expression (5) only in reference to the lowest age at first capture, i.e., when $t_{\rho'} = 0$; it is also formally equivalent to von Bertalanffy expressions (for length-on-age, however, rather than weight-on-age). Such relationships have been termed "monomolecular" (cf. Defares and Sneddon 1961, p. 228). All three growth functions are graphed in Figure 1. Expressions (3) and (4) are based on Doi's; like (5), these ascribe an initial weight of 1.00 kg and a final weight of 1.76 kg to pink salmon in their last 4 months of ocean life. The intervening growth patterns are different, however; under expression (3) growth follows a simple exponential pattern with a monthly coefficient of increase of 0.1419 (cf. Ricker's g), while under (4) the growth pattern is linear with a monthly weight gain of 19%.

Absolute inshore yield (Y_c) from 1,000 recruits alive 4 months before return is simply the product of the survivors from natural mortality offshore (with offshore fishing absent), mean weight per fish at return, and the inshore rate of exploitation (E_c). Assuming that natural mortality during inshore fishing is absent, the instantaneous rate of inshore fishing mortality (F_c) equals $-\ln(1-E_c)$. In the presence of offshore fishing, the return from a given number of recruits is naturally reduced and a lower inshore exploitation rate is called for if a like number of spawners is to be protected in either case. To obtain the desired survival implies that

$$P/N_0 = e^{-M-F_o} = (e^{-M})e^{-F_c} = \\ = (e^{-M-F_o'})e^{-F_c'}, \qquad (6)$$

depending on whether this is to be achieved by removing the excess before return, after return, or during both periods. In the present paper, as well as in Doi (1962), natural mortality and wastage are assumed to be absent during the inshore phase of exploitation.

To simulate offshore yields under conditions of positive, equal, or negative balance between growth (at $g = 0.1419$/month) and natural mortality during the offshore phase, values of $M = 0.5\ g$, $1.0\ g$, and $1.5\ g$ were chosen. A fourth value ($M = 0.10$) was also considered since this is Doi's current estimate for Far Eastern pink salmon during the last 4 months at sea. A hypothetical level of escapement ($P/N_0 = 0.113$) is used in the present discussion; (it would be obtained if $M = g = 0.1419$ and exploitation were to affect 80% of the recruits). The target level of escapement used by Doi (1962), and others entering his computations of yield, are greater than 0.113 and will be considered in detail in the section on combined yield.

In its most general form, Doi's index of rationality of offshore fishing is

$$I = \frac{Y_o' + Y_c'}{Y_c} = \frac{\left\{\begin{matrix}\text{Offshore catch} + \\ + \text{ Subsequent inshore catch}\end{matrix}\right\}}{\left\{\begin{matrix}\text{Inshore catch with offshore} \\ \text{fishing absent}\end{matrix}\right\}} \qquad (7)$$

His application of the index is subject to the double restriction $E_c = E_c' = 0.50$ which affects both numerator and denominator in (7). The restriction $E_c = 0.50$ on the denominator leads to the expression of combined yields in units that equal the current inshore catch of pink salmon under combined exploitation. An alternative unit, more directly related to the reproductive requirement of salmon stocks, would equal the yield realized from the removal of the harvestable excess, either inshore or offshore. In terms of stock definition, the choice of inshore equivalents seems preferable; expressed as a relation between inshore quan-

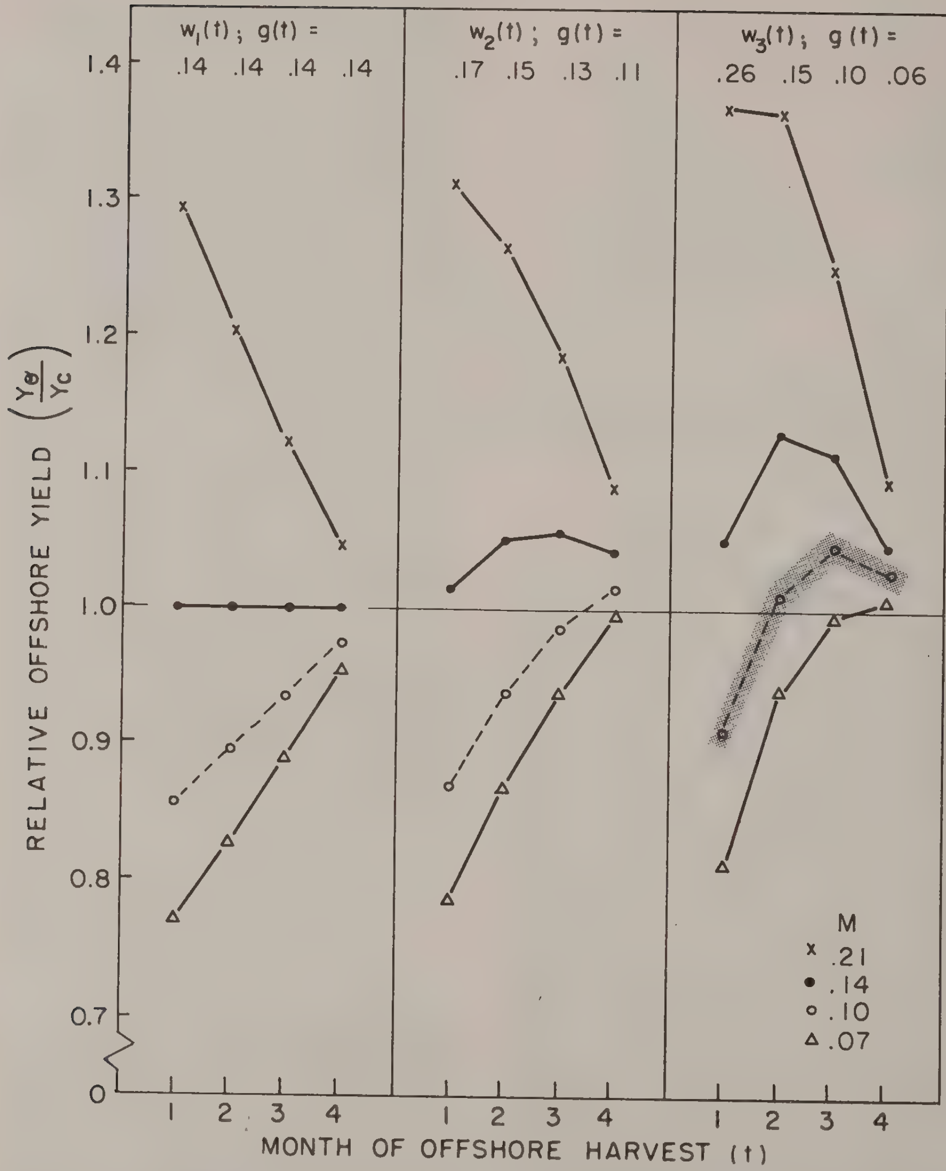

FIGURE 2.—Variation in relative offshore yield (Y_o/Y_c) due to timing of the month of exploitation when $P = 113$ and $k = 0$. Monthly coefficients of weight increase under each growth assumption $w(t)$ are shown across the top; those of natural mortality (M) are identified by symbols. The implicit values of F_o and F_c within each plot are equal by equation (6).

tities, they can be written as the inshore yield (Y_c) when $E_c = 1.00 - (P/N_4)$, or thought of as the inshore yield ". . . if a coastal fishery exists that is capable of taking the optimum percentage of a salmon stock . . ." (Ricker, 1962, p. 539).

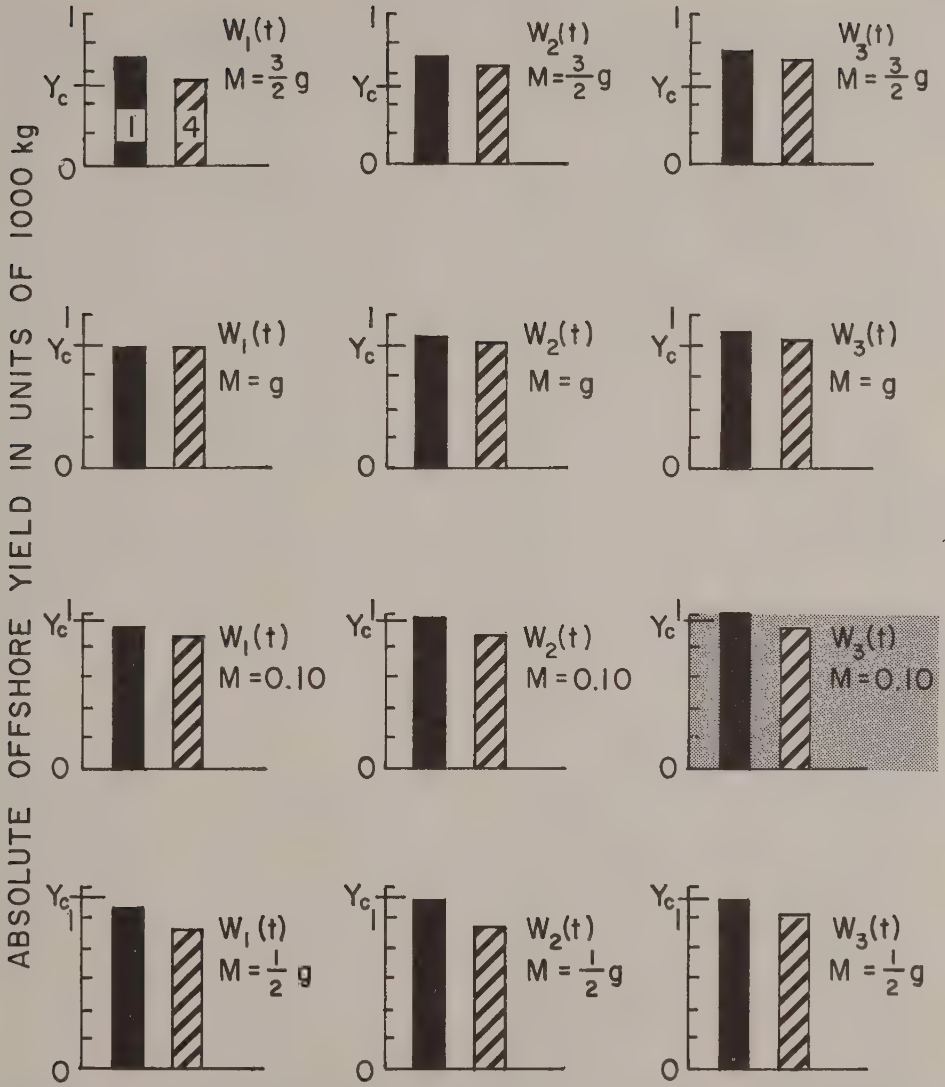

FIGURE 3.—Reduction of relative offshore yield (Y_o/Y_c) due to extending the term of offshore exploitation from the best single month to 4 months. Parameters as for Figure 2 except F_o is now $4F_o$, $g = 0.1419$.

EFFECT OF TIMING OF EXPLOITATION AND WASTAGE ON RELATIVE OFFSHORE YIELDS

In this section relative offshore yields (Y_o/Y_c) are compared under various sets of natural conditions $\{w(t), M\}$, and conditions of exploitation $\{F_o, \tau, k\}$. In these comparisons the parameters of inshore and offshore fishing have been chosen so as to account (with M) for the entire excess over a hypothetical target escapement of 113 spawners per 1,000 recruits. If the instantaneous offshore fishing mortality rate and the biomass mean refer to the same unit of time, and if wastage is absent, the values Y_o and Y_c represent like fractions of biomass means (since $F_o \equiv F_c$). Thus ratios of Y_o and Y_c are equivalent to

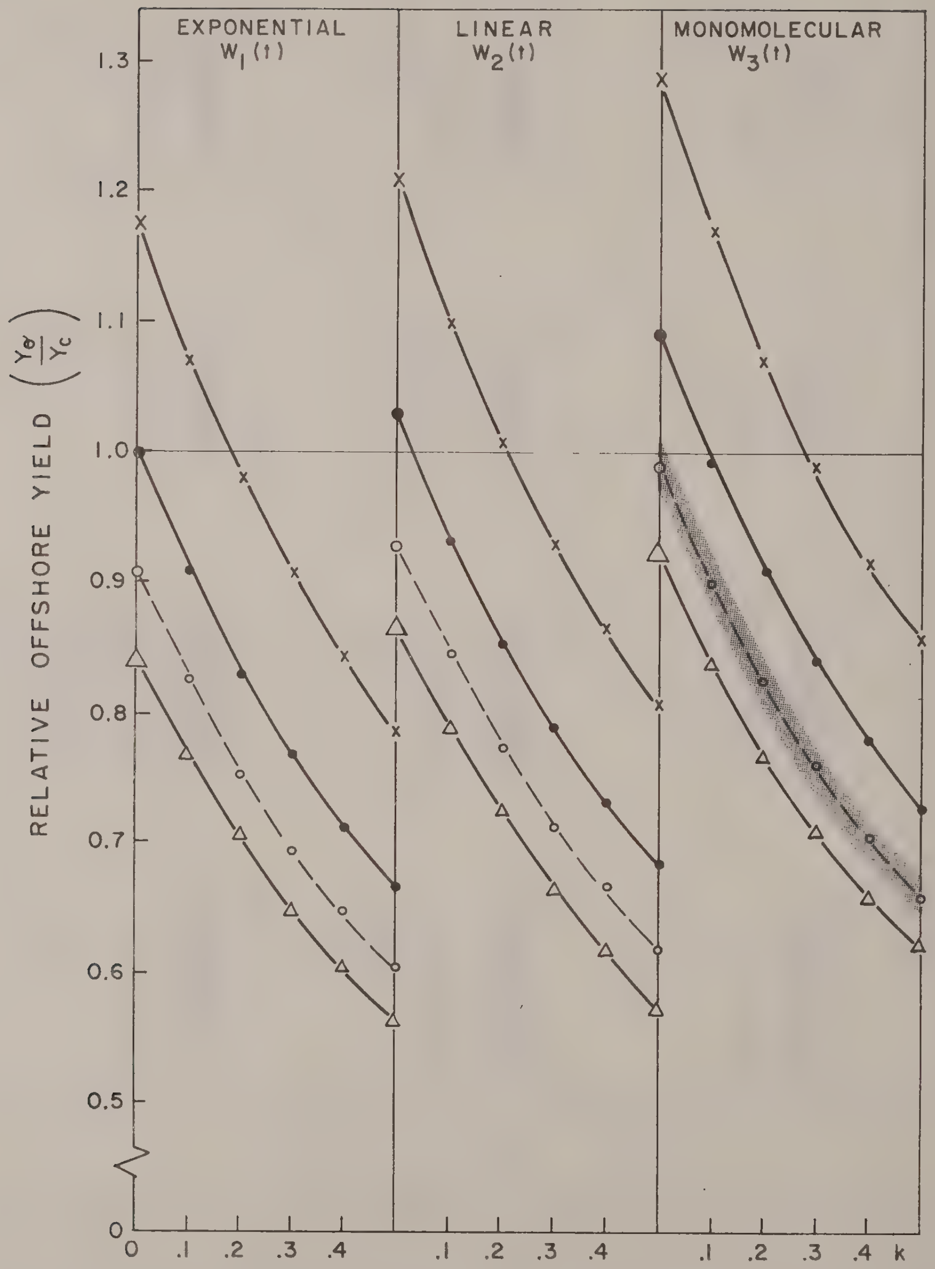

FIGURE 4.—Reduction of relative 4-month offshore yields (Y_o/Y_c) due to wastage (fish killed but not captured). Implicit parameters as for Figure 2 except F_o is now $4(1+k)F_o$.

those of mean biomass over the offshore and inshore phases of exploitation, respectively.

Relative 1-month offshore yields indicate generally the presence of a maximum which is specific with respect to month of occurrence. Figure 2 contains a series of plots of four points representing single-month yields during consecutive months, under different sets of natural conditions. One of the plots ($M = g = 0.1419$) shows Ricker's special case in which a maximum fails to develop and the relative offshore yield is unity regardless of month fished. In all other cases maxima are indicated, with the month of occurrence differing according to natural conditions (growth and natural mortality). Among the latter, the set with $M = 0.10$ and the monomolecular growth assumption $w_3(t)$ refers to Far Eastern pink salmon (shaded plot in Figure 2, also 3 and 4): the maximum relative offshore yield is 1.04 and occurs during the third month of offshore vulnerability, i.e., the second month preceding the return of the run to inshore waters.

An equivalent amount of offshore fishing distributed over more than a single month would produce some average of the values shown in each plot, with the reduction from maximum depending on natural conditions and the timing of exploitation in relation to the month of maximum bulk. Reductions due to 4-month terms are shown in absolute weight per 1,000 recruits (Figure 3); these refer to the same sets of natural conditions as Figure 2. Again referring to $w_3(t)$, $M = 0.10$, the absolute offshore yield is now slightly lower than the unconditional inshore yield.

An additional cause of reduction in offshore yield arises when wastage (i.e., dropouts of dead fish from nets fished on the high seas) enters the fishing process. The effect on 4-month yields is shown in Figure 4. The reductions are according to $1/1 + k)$, where k is the coefficient of wastage associated with the particular type of gear used. Omission of this factor could be misleading, especially when the natural balance between growth and mortality is assumed to be negative. For example, if wastage is presumed absent and $M = 1.5\ g$, Figure 4 suggests that offshore yields without wastage exceed inshore yields by between 19 and 30%, depending on the growth assumption used; however, the same plots also show that a wastage coefficient of 0.3 would be sufficient to offset such advantages, or exceed them, regardless of the growth pattern selected. A somewhat higher value, $k = 0.4$, would offset similar advantages of the maximal values of 1-month offshore yields in Figure 2. However, the fishing intensity needed to remove the excess in a single month at sea would be much larger than the current level as estimated by Doi (1962). Rationality has been claimed by him for certain combinations of inshore and offshore fishing in which the coefficient of wastage attending offshore fishing is as high as 0.5.

COMBINATIONS OF OFFSHORE AND INSHORE YIELD

In Doi's treatment of the yield problem, offshore operations were examined only in conjunction with a single value of inshore exploitation rate and interest centered on how offshore variations in starting date and intensity of fishing would affect combined yields of this sort. (Unconditional offshore yields as in Figures 2 to 4 were not gone into, and neither fishing component was considered at levels high enough to remove the available excess over any specified target escapement.)

In this section combined yields are examined by first reviewing some of Doi's results. One of his restrictions on inshore fishing, ($E_c = E_c') = 0.50$, is then replaced by one on offshore fishing, which also derives from his description of current joint exploitation, and the resulting, more general form of Doi's index is displayed with the second restriction ($E_c = E_c'$) being retained. Following this, combined yields are displayed when all special restrictions on inshore or offshore fishing intensity are removed and total fishing intensity is limited only by the requirement that a specified fraction of the recruits survive to spawn.

Doi's method

Doi's standard for measuring the rationality of offshore fishing under any set i of offshore conditions is given by the excess over unity in

$$I = \frac{[(t_c - t_{\rho'})F_o'B_o'(i) + E_c'B_c'(i)]}{E_cB_c};$$

$$E_c = E_c' = 0.50. \qquad (8)$$

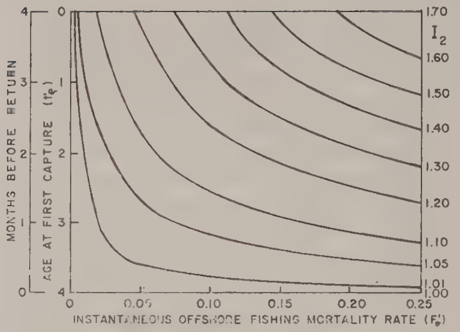

FIGURE 5a.—Yield isopleths in terms of the index I, described by formula (8), for $\{M, k, E_c'\} = \{0.25, 0.50, 0.50\}$ and the monomolecular growth assumption. This figure may be compared with Figure 4c in Doi (1962).

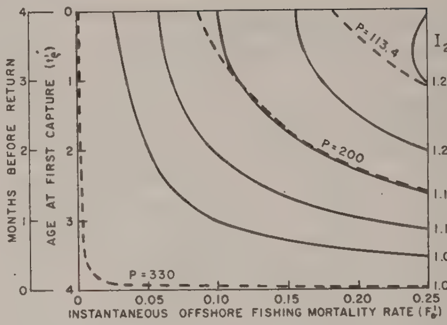

FIGURE 5b.—Yield isopleths in terms of the index I, described by formula (8), using the estimate of M emphasized by Doi (1962). Implicit parameters as in Figure 5a except M is now 0.10. In the absence of offshore fishing, 335 fish per 1,000 recruits would survive to spawn.

where i is the set of parameters for growth $(w(t))$, offshore natural mortality (M_o), offshore fishing mortality (F_o'), coefficient of wastage (k), and age at first capture $(t_{\rho'})$. All offshore fishing periods extend to t_c, and B_c is the biomass of the return when offshore fishing is absent.

Isopleths for one of the sets given by Doi—his Figure 4c, representing the set i with $w(t) = w_3(t)$, $M = 0.25$, F_o' as shown, $k = 0.5$, and $t_{\rho'}$ as shown—are reconstructed in Figure 5a and agreement is indicated for 4-month terms of offshore exploitation, i.e., $t_{\rho'}$ equals zero.[1] Along either axis the index assumes the value 1.00 since the numerator in (8) reduces to E_cB_c when offshore fishing is absent.

Figure 5b includes sets of natural conditions $\{w(t) = w_3(t),\ M = 0.10\}$ and conditions of exploitation $\{F_o' = 0.10,\ k = 0.50,\ t_{\rho'} = 0\}$, which were viewed by Doi as warranting combined inshore and offshore exploitation, and contains the particular value of I derived below in order to demonstrate some details regarding the computation of isopleth values and their interpretation. At $F_o' = 0.086$ and $t_{\rho'} = 0$, the numerator of (8) is given by the sum of

$$Y_o' = 4F_o'N_0 \int_0^1 w_3(t)e^{-4[M+(1+k)F_o']\tau_1}\, d\tau_1$$
$$= 317.1 \text{ kg},$$

and

$$Y_c' = E_c'w_3(4)N_4$$
$$= (0.50)(1.764)1{,}000e^{-4[M+(1+k)F_o']}$$
$$= 352.9 \text{ kg};$$

dividing by the inshore yield achievable in the absence of prior offshore fishing gives

$$I = 670.0/(0.50)(1.764)1{,}000e^{-4M} = 1.13,$$

as indicated along the top margin of the figure (interpolate between $I = 1.10$ and $I = 1.15$, corresponding to $t_{\rho'} = 0$ and $F_o' \cong 0.09$).

Considering Doi's restriction on inshore fishing, this particular combination of duration and intensity of offshore fishing may be viewed as optimal from the standpoint of removing the harvestable excess over $P = 200$ with a minimum of offshore gear. Optimality with respect to yield is doubtful, however. That the index number exceeds unity ($I = 1.13$) is uninformative, in this regard, since the value of Y_c includes but a part of the harvestable excess: given $M = 0.10$ and $E_c = 0.50$, the number of spawners surviving would be 335, rather than 200, per 1,000 recruits. Thus, two different spawner restrictions are involved in Doi's index, and the lower of these implies an unconditional inshore exploitation rate of 70% rather than 50% as specified. As a result the isopleths of Figure 5b are scaled upward by a factor of 0.70/0.50, or 1.4. Dividing the associated index numbers by 1.4 makes it apparent that the figure contains no effort combinations whose yields are superior to those achievable when $M = 0.10$ and $P/N_0 = 0.200$, as supposed in Doi (1962), and when all fishing is confined to inshore waters. Furthermore, the location of the escapement line for $P = 330$ points indirectly to the absence of feasible additions of offshore effort, if the second spawner restriction in Doi's index, i.e., $P/N_0 = 0.335$ is a realistic one biologically.

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[1] Differences were found for higher ages at first capture. These are believed to affect some of the author's conclusions.

Alternative restriction on offshore fishing mortality rate (F_o')

One of the restrictions on inshore fishing in (8) may be exchanged for a similar one on offshore fishing, which may be chosen so that offshore fishing is at its current level of intensity ($F_o' \cong 0.10$), and covers all 4 months of offshore vulnerability. Then

$$I_1 = \frac{4F_o'B_o'(i) + E_c'B_c'(i)}{E_cB_c};$$
$$E_c = E_c',$$
$$i = \{w_3(t), 0.10, F_o' = 0.10, 0.50, 0\}. \qquad (9)$$

The results are shown in Figure 6. The straight line on which I_1 is plotted is itself the relation between combined yield and inshore exploitation rate when the size of the offshore catch is fixed. I_1 is seen to vary inversely with absolute yield, indicating that yield may be associated with increasing or decreasing index numbers as the exploitation rate is held constant inshore as in Figures 5a, b, or offshore (Figure 6). The latter figure also suggests that the fishing combination with $E_c' = 0.50$ is not quite compatible with $P = 200$: the resulting escapement would fall 8% short of target. On the other hand, under a lower spawner requirement, the same combination of effort may not remove all of the harvestable excess. Using $P = 113$ for illustration, one of many different possible corrections from this standpoint could be obtained by fishing offshore alone so that $\{F_o', E_c'\} = (0.295, 0)$, since $1{,}000 \exp -4[0.10 + (1 + 0.5)0.295] = 113.4$; or by inshore fishing alone at $E_c = 0.83$, since $(1 - 0.83)\ 1{,}000 \exp -4M = 113.4$; or by the appropriate combination for $P = 113.4$ in Figure 6. It will be shown that such modifications, though equivalent with respect to P, produce different yields.

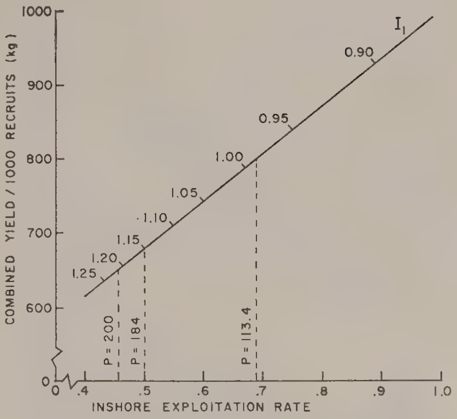

FIGURE 6.—Relation of I_1 (the generalized form of Doi's index described by formula (9)) to absolute combined yield when offshore, rather than inshore fishing is restricted to a single level of exploitation ($F_o' = 0.10$). Implicit offshore parameters are $\{M, F_o', k, \tau\} = \{0.10, 0.10, 0.50, 4\}$, with monomolecular growth assumption. The inshore exploitation rate shown is the same with offshore fishing present, or absent ($E_c \equiv E_c'$).

Combined yields in units of harvestable excess

Since neither I nor I_1 includes a referent to total harvestable excess, the denominator of the index needs to be altered so as to equal the unconditional inshore yield under a specific target escapement. For $P = 113$, I_1 becomes

$$\left.\begin{aligned} I_2 &= \frac{4F_o'B_o'(i) + E_c'B_c'(i)}{E_cB_c} \text{ with} \\ E_c &= \frac{N_4 - 113.4}{N_4} = 0.83, \\ i &= \{w_3(t), 0.10, F_o' = 0.10, 0.50, 0\} \end{aligned}\right\} \qquad (10)$$

Figure 7 shows the effect of this change for the same set of conditions as the preceding figure. The new index is linear with respect to yield and inshore exploitation rate. When E_c' equals 50%, a yield loss of 31% from $Y_c = E_cB_c$ is implied by $I_2 = 0.69$ (but not by $I_1 = I_2 \times 0.83/0.50 = 1.15$ in Figure 6, or in Figure 5b); when E_c' equals 69%, the loss is reduced but the yield remains suboptimal as indicated by $I_2 = 0.82$.

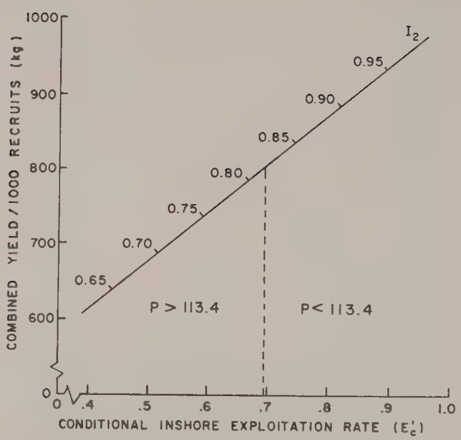

FIGURE 7.—Combined yields of Figure 6 expressed in units of harvestable excess (i.e., inshore yield Y_c when the escapement is 113 spawners/1,000 recruits). For I_2, see formula (10).

Altering the denominator of Doi's index as in (10) amounts to applying Ricker's standard of comparison to combined yields. The latter may be graphed as a function of both inshore and offshore fishing, e.g., E_c' and $(t_c - t_{p'})F_o'$, without restricting either to a particular level. Since interest resides in yield relations that do not interfere with the reproductive requirements of exploited stocks, expression (10) may be generalized to

$$I_2 = \frac{4F_o'B_o'(i) + E_c'B_c'(i)}{E_cB_c};$$

$$\frac{P}{N_0} \geqslant (1-E_c')e^{-4[M+(1+k)F_o']}. \qquad (11)$$

Under the new restriction each solution space refers to only one level of escapement, but the range of conditions shown includes the range emphasized by Doi (and shown by the broken perpendiculars on $E_c' = 0.50$ in Figures 8 and 9); also included are the two conditions compared by Ricker (1964), i.e., wholly inshore fishing versus wholly offshore fishing. The latter conditions are represented by the extreme points of each solution space. For $P = 113.4$, the results of this modification appear in Figure 8. A change in combined exploitation from $(F_o', E_c') = (0.10, 0.50)$ to $(0.10, 0.69)$ is now seen as one of many solutions satisfying P. At one of the extreme points $(0.295, 0)$, the index value $I_2 \cong 0.65$ suggests that only about two-thirds of the potential yield would be achieved.[2] The isoline for $I_2 = 1.00$ is seen to be the other extreme point of the solution space $(E_c' = E_c = 0.83)$. At this point the yield is maximal and the spawner requirement is satisfied so that the solution may be considered as optimal in this sense.

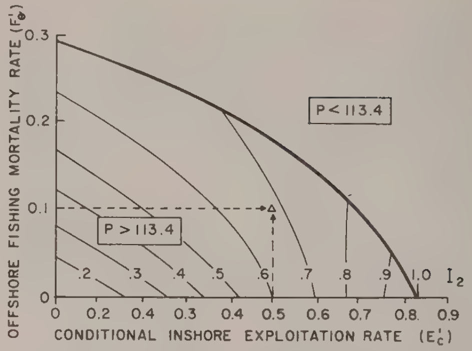

FIGURE 8.—Far Eastern pink salmon isopleths (I_2) as function of inshore and offshore fishing effort, in units of harvestable excess (Y_o) when $P/N_o = 0.113$. Implicit offshore parameters $\{w(t), M, k, \tau\}$ are $\{w_3(t), 0.10, 0.50, 4\}$.

The hypothetical restriction $P = 113.4$ used here for illustration may not be realistic in the stocks considered by Doi (1962). If the spawner requirement is satisfied by $E_c = 0.50$ in formula (8), as many as 335 pink salmon/1,000 recruits may be needed for spawning, as few as 184 if $\{F_o', E_c'\} = \{0.10, 0.50\}$ as suggested by Doi, or 200 according to the consensus he cites regarding spawner requirements. On the other hand, inshore exploitation rates exceeding 50% may be technically as feasible in Asian waters as, for instance, off British Columbia where inshore fishing accounts commonly for 50 to 70% of pink salmon returns (Neave, 1953).

The survivors from such (unconditional) inshore operations are considered as target escapements under the same natural conditions and wastage as before (Figure 9 a to c). Doi's index and I_2 differ in base except when $P = 335$; for this case Figure 9c illustrates a

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[2] This particular combination appears also in the shaded plot of Figure 4 as the relative offshore yield for $w_3(t)$, $M = 0.10$, $k = 0.50$ and $4(1 + k)$ $(0.295) = 1.77$. The left extreme of the same plot suggests lower yields regardless of the actual level of wastage.

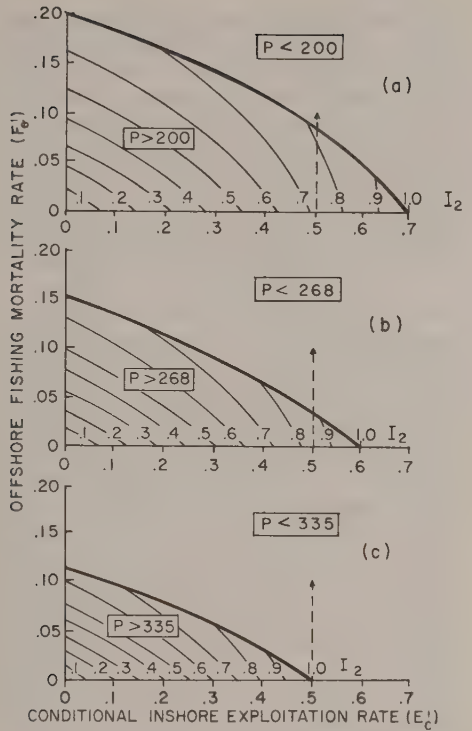

FIGURE 9.—Far Eastern pink salmon isopleths (I_2), in units of harvestable excess (Y_c) under each of three levels of target escapement (P). Implicit offshore parameters as in Figure 8.

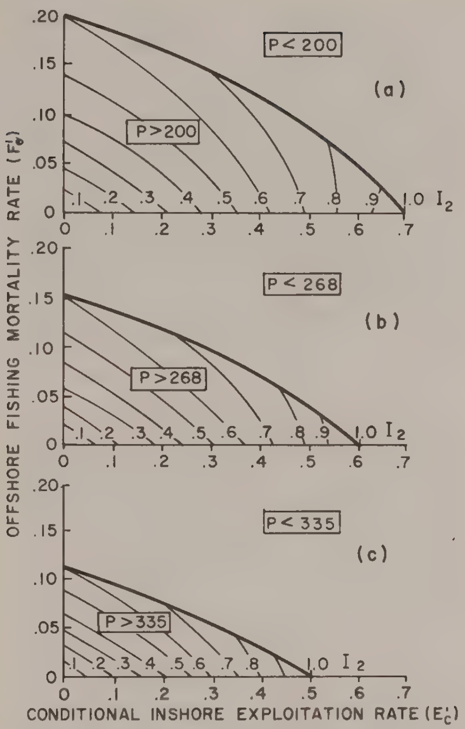

FIGURE 10.—Far Eastern pink salmon isopleths (I_2) as in Figure 9, except for substitution of $w_3(t)$ by the exponential growth function $w_1(t)$.

point made earlier in connection with Figure 5b: given an inshore exploitation rate of 50%, feasible additions of offshore effort are absent. The broken line in Figure 9c locates the "rational" solutions appearing along the top margin of Figure 5b as lying outside the feasible solution space.

Feasible effort combinations do exist when $P = 200$ and $E_c' = 0.50$, but these are suboptimal with respect to yield (Figure 9a). Only 72% of optimum is achievable if offshore fishing were eliminated but inshore exploitation retained at 50%. This is of some interest in view of Doi's corollary to his own definition of rational offshore exploitation: "If offshore fisheries are found diminishing the total yield under any circumstances as to the duration of the fishing season and the amount of effort, they should be prohibited from operating in the future." The figure illustrates that the suggested course of action would not achieve optimality without appropriate modification of the inshore exploitation rate.

The general distribution of yield contours included in Figures 9a to c varies with spawner requirement as well as distribution of effort. For example, given the effort combination $\{F_o', E_c'\} = \{0.05, 0.20\}$, the index value I_2 changes from 0.60 to 0.45 as P changes from 335 to 200. This suggests that more productive runs, i.e., those with a relatively large harvestable excess, would be less efficiently harvested by combined inshore and offshore fishing than runs whose harvestable excess is small.

The effect of exponential, rather than monomolecular growth (with all other conditions unchanged from Figure 9) is shown in Figure 10. The absence of an offshore maximum of biomass in this case is reflected by compara-

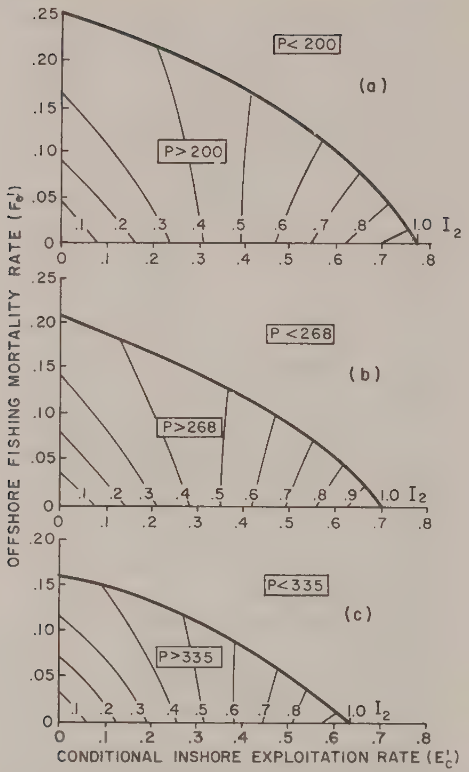

FIGURE 11.—Combined yield isopleths (I_2) using estimates of average growth rate and natural mortality in Central British Columbia pink salmon (based on Ricker, 1964, table XII). Implicit offshore parameters $\{w(t), M, k, \tau\}$ are $\{w_{t-1}e^{0.30}, 0.02, 0.50, 4\}$

tively lower values of I_2 within each solution space. The boundaries themselves are unchanged from the preceding figure since they are functionally unrelated to growth.

Estimates of growth and natural mortality rates for North American stocks of pink salmon differ substantially from those attributed to Far Eastern stocks by Doi (1962). According to LeBrasseur and Parker (1964), mean exponential weight growth of central British Columbia stocks of pink salmon during the 4 months before reaching inshore waters is given by $g \cong 0.30$ per month, while the exponential rate of natural mortality has been estimated at no more than $M = 0.02$ per month (Ricker, 1964). In Figure 11, the latter parameter values replace Doi's estimates of $w(t)$ and M. For the same target escapements as before, the values of I_2 are much lower for corresponding effort combinations than those in Figures 9 and 10. The relative offshore harvest, i.e., the highest (biologically) admissible 4-month offshore yield, is now about one-third of the highest admissible inshore yield, compared to about two-thirds in pink salmon stocks of the Northwestern North Pacific.

IMPLICATIONS FOR MANAGEMENT

When an unfished salmon run attains its maximal weight before return to inshore waters, and inshore harvest of the excess over the target escapement is technically feasible, the rationality of offshore fishing may depend critically on the wastage characteristics of the offshore catching method. The present findings agree with Doi's in this respect, although the growth–mortality balance did not enter as such into the development of his criterion for determining the rationality of offshore exploitation. Whether this balance is a negative one in Far Eastern stocks of pink salmon remains a moot point in the absence of documentation regarding the estimates of either of these parameters.

For combinations of growth and natural mortality rates that result in maximal biomass offshore, the maximum is time-specific and fishing needs to be of appropriate timing and intensity to avoid suboptimal forms of exploitation. In Doi's case, a 4-month term of offshore fishing has been suggested; it has been shown that such an extension of time fished is likely to depress offshore yield to a point lower than could be achieved by confining all fishing to inshore waters, even if it be assumed that wastage at sea is absent and that growth follows the pattern suggested by Doi.

It will have been noted that Doi's restriction on inshore fishing makes his concept of rational exploitation independent of stock productivity. His criterion is such that combined yields may be considerably less than the maximum sustainable yield, yet judged to be rational or optimal. As has been shown here, his restriction eliminates from comparison a rather large class (of effort combinations) which is equally feasible in regard to the protection of spawners but implies substantially higher sustainable yields. Doi considered a near-optimal effort combination to be one which protects 200 spawners per 1,000 recruits and operates at exploitation rates of 22% offshore and 50% inshore; yet total production from this scheme remains capable of a 22% improvement (Figure 9a, $F_o' = 0.086$). A similar scheme applied to central British Columbia pink salmon is likely to prevent an 80% improvement in sustainable yield (Figure 11a).

The existence of superior effort combinations and the degree to which the yields considered by Doi depart from optimality are points emphasized in the present paper (Figures 6 to 11). This was done by (1) a change in the variables displayed, (2) by admitting, in principle, any combination of offshore and inshore fishing to comparison, and (3) by using an index which is based on the reproductive requirement of the exploited runs and compatible with Ricker's formulation of the yield problem. For Far Eastern runs of pink salmon it has been shown that the transfer of any part of the highest (biologically) admissible inshore fishing effort is likely to depress the sustainable yield, with spawner requirements anywhere between 17 and 50% of the unfished return and the possible presence of a natural maximum of biomass offshore notwithstanding.

Independent of the presentation and discussion of his index, Doi (1962) alluded to the existence of "best" yields associated with single-component fisheries, either inshore or offshore. The present method would permit recognition of optimal yield relations in either event.

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Ellobiopsidae of Alaskan Coastal Waters

ETHELWYN G. HOFFMAN and ROBERT M. YANCEY[1]

ABSTRACT: Four species of ellobiopsids were taken in Alaskan coastal waters. *Thalassomyces fagei* (a synonym of *Amallocystis fagei*) was found to parasitize specimens of the euphausid *Thysanoessa raschii* taken in Kachemak Bay, Alaska. The development of *T. fagei* external to the host from a small knob to the mature form was found to occur by repeated dichotomous branching. *T. fagei* occurred during April and May but was not observed at other times of the year. *Thalassomyces* sp. was found to be parasitic on specimens of the mysid *Acanthomysis pseudomacropsis* taken in Kachemak Bay, Alaska. The range of *Thalassomyces capillosus,* parasitic on the caridean *Pasiphaea pacifica,* is extended from Coos Bay, Oregon, to Orca Bay, Prince William Sound, Alaska. *Ellobiopsis chattoni* was found to parasitize the copepod *Metridia longa,* a new host of this ellobiopsid. Specimens of *E. chattoni* were taken in the waters of southeastern Alaska, extending the range of *E. chattoni* from the Atlantic to the north Pacific.

THE SYSTEMATIC POSITION of the family Ellobiopsidae Coutière and the genera therein has been an enigma since their original description. According to Margaret Jepps (1937), T. Scott in 1897 first described the ellobiopsid now known as *Ellobiopsis chattoni* as a "? infusorian parasite" of the copepod *Calanus finmarchicus.* She states also that in 1910 Caullery associated the ellobiopsids with the Dinoflagellata. Various authors have continued to consider these organisms to be closely related to the dinoflagellates. Jepps points out that a relation with the fungi is possible. Boschma (1949, 1956, and 1959) reviewed the entire group and preferred to consider them as "Protista of uncertain position." He noted that the ellobiopsids have affinities with the following groups: parasitic peridinians, flagellates, and possibly fungi of the family Saprolegniaceae, and that the group is made up of a number of heterogeneous elements.

The family Ellobiopsidae is a rather heterogeneous group consisting of several genera. Members of the genus *Ellobiocystis* are epibionts, whereas members of the genera *Ellobiopsis* and *Thalassomyces* are parasites. This study is concerned only with the last two genera. Various pelagic crustaceans, including copepods, euphausids, and carideans, are hosts of species of *Ellobiopsis* and *Thalassomyces.*

Organisms of the genus *Ellobiopsis* parasitize several species of copepods. Various species of *Calanus* have been reported by Marshall et al. (1934), Marshall and Orr (1955), and Jepps (1937) to be parasitized by *Ellobiopsis chattoni. Pseudocalanus* (Marshall, 1949), *Clausocalanus* (Hovasse, 1951), *Acartia* (Boschma, 1956), and *Metridia,* in this work, have also been found as hosts of *E. chattoni.*

Jepps (1937) described very early forms of this parasite which she found on the antennae and mouth parts of *Calanus finmarchicus.* These first appeared as small knobs on the setae of the mouth parts. At maturity *E. chattoni* consists of a pear-shaped part, the trophomere, which is attached by a stalk to the host's appendage. Distal to the trophomere there may develop one or two rounded segments, the gonomeres, in which sporulation takes place. According to Jepp's description of sporulation in *E. chattoni,* small buds arise on the free surface of the gonomere, each of which undergoes a series of fissions, forming spores. The mechanism of spore release and the relation between free spores and the occurrence of small knobs on the host appendages is unknown.

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[1] U. S. Bureau of Commercial Fisheries Biological Laboratory, Auke Bay, Alaska. Manuscript received August 20, 1964.

Species of *Thalassomyces* (formerly known as *Amallocystis*) are different in many respects from those of *Ellobiopsis*. Each *Thalassomyces* consists of a tuft of trophomeres extending from a central stalk, whereas each *Ellobiopsis* has only one trophomere. The number of trophomeres extending from the stalk is used as a species-differentiating character in *Thalassomyces*.

The gonomere (or gonomeres) which forms on the distal end of the trophomere is separated by a septum from the trophomere. Individuals of *Ellobiopsis* species have one or two gonomeres. If more than one gonomere is present, as in the *Thalassomyces* species and some *Ellobiopsis* species, each is separated from the next by a septum. Sporulation has not been described for any *Thalassomyces* species but is assumed to occur. Old individuals of *Thalassomyces* spp. may be found with numerous empty gonomeres; some with collapsed walls may remain attached to the trophomere.

Various euphausids, mysids, and carideans have been reported as hosts for *Thalassomyces* species. The ellobiopsid may be attached ventrally to the host's abdomen, as in *T. racemosus,* to the dorsal surface of the carapace, as in *T. fagei* and *Thalassomyces* sp., or at the base of the rostrum, as in *T. capillosus* (Boschma, 1956).

As a result of this study the ranges for three species of ellobiopsids have been extended to Alaskan waters. They are *T. fagei, T. capillosus,* and *E. chattoni. T. capillosus* is the only species of the three previously recorded in the north Pacific Ocean. The development of *T. fagei* is described, and seasonal distribution of this species is discussed. *Metridia longa* was found to be a host for *E. chattoni.*

OBSERVATIONS AND DISCUSSION

Thalassomyces fagei

The genus was named *Amallocystis* until 1959, when Boschma pointed out that, because of its priority, *Thalassomyces* is the valid name.

The euphausid *Thysanoessa raschii* (M. Sars) has been recorded as host for this ellobiopsid on two previous occasions. Einarsson (1945) described *Amallocystis* sp. parasitic on *T. raschii* taken in May in Faxafloi to the west of Iceland. Boschma (1949) established that the *Amallocystis* sp. of Einarsson was *A. fagei* (Boschma), and later (1959) he corrected the generic name to *Thalassomyces*. Glover (1952) observed two specimens of this euphausid infected with *T. fagei*. One was taken in July and the second in August of 1948 in the region of May Island in the Firth of Forth. Initially *T. fagei* (Boschma) was described as an Antarctic species, but its distribution has been extended to include the northern Atlantic waters by reports of Einarsson (1945), Glover (1952), and Macdonald (1927). Macdonald reported the occurrence of *Staphlocystis racemosus* on the euphausid *Meganyctiphanes norvegica* taken in the Clyde Sea. Boschma (1949) believes that this ellobiopsid was *T. fagei* and not *S. racemosus.*

In our investigation we also found *T. fagei* parasitic on *Thysanoessa raschii.* The specimens were taken during the spring of 1963 in three small inlets which are part of Kachemak Bay, Alaska (59°27′N, 151°33′W). The samples were taken in 20-minute oblique hauls of a ½-m plankton net with a standard No. 2 mesh. The depth in the area did not exceed 53 fathoms. This is the first record of this species of ellobiopsid from the Pacific Ocean, and its range is thus extended from the Atlantic to the northeastern Pacific.

The ellobiopsid parasites are attached to the host by a stalk which extends through the dorsal side of the carapace and penetrates the tissues below. The parasite is located in a dorsal concavity on the carapace of the host which is not found in uninfected euphausids (Fig. 1). An infected *T. raschii* usually bears only one *Thalassomyces,* although up to four were observed. A specimen bearing two parasites is shown in Figure 2.

The mature parasite has 30–50 trophomeres which are ramifications of the single central stalk. The trophomeres are expanded distally into a club shape. Trophomeres with one to six gonomeres were observed, although more commonly three to five occur. The gonomeres are spherical to slightly elliptical in shape. Figures 3 and 4*f* are a photograph and a camera lucida drawing respectively of a mature parasite. In older individuals some of the distal gonomeres are empty. The gonomere remnant may break

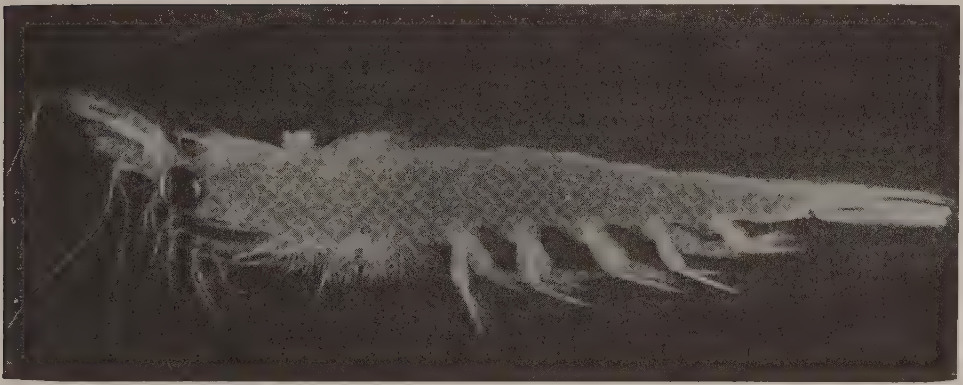

FIG. 1. A young ellobiopsid located in a concavity on the dorsal side of host's carapace.

off, leaving a small tuft, or the walls may collapse, producing a filament hanging from the end of a more proximal gonomere (Fig. 4*f*). Jepps (1937) has observed that in *Ellobiopsis chattoni*, parasitic on *Calanus finmarchicus*, this condition of the gonomere is the result of sporulation. She noted that when all the spores have been released, the test of the distal segment either degenerates or is left full of debris.

The development of *Thalassomyces fagei* was worked out from a sequence of specimens taken in various stages of growth (Fig. 4). The ellobiopsid was removed from its host and placed with the stalk extending upward to facilitate drawing. The illustrations show this aspect of the parasite, except Figures 4*a* and 4*b*, which are views from one side. All the drawings were done with the aid of a camera lucida.

It is not known whether the initial infection by the parasite is located internally or externally. Jepps (1937) hypothesized that *E. chattoni* initially penetrates the host from the outside. In the material of *Thysanoessa raschii* examined in the present study, *Thalassomyces fagei* was found to have a well-established internal structure at the earliest stages in its external development. Figure 4*b* is a lateral view of *T. fagei* shown extending through the host carapace. The structure in the lower left is the "sieve plate" of Boschma (1949). Numerous protoplasmic excrescences protrude through openings in the cuticle of the ellobiopsid. These excrescences are thought to be the organ of absorption of food for the parasite.

The major function of the external structure of the parasite is assumed to be reproductive.

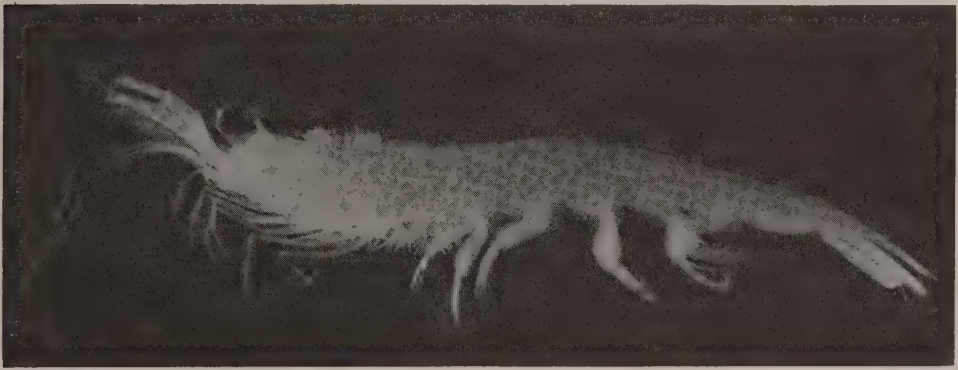

FIG. 2. Euphausid with two discrete parasites.

Whether reproduction is sexual or asexual is unknown. These observations agree with the hypothesis accepted by Boschma (1949) for *T. fagei* concerning the assumed release of spores from the gonomere. Jepps (1937) described sporulation in the distal structure which she termed the gonomere of *Ellobiopsis chattoni.* Hovasse (1951) observed sporulation of *E. fagei.* No observations of sporulation in a *Thalassomyces* species are available.

The external development of *T. fagei* is initiated by a small knob-shaped structure appearing through the middorsal region of the carapace of the host. This single knob bifurcates slightly, producing a bilateral structure (Fig. 4*a*). The next stage appears to be the result of simultaneous bifurcation of each of the previously formed lobes, resulting in a four-lobed structure (Fig. 4*c*). Further development of *T. fagei* is accomplished by repeated simultaneous dichotomous branching of each of the existing lobes. The simultaneous nature of the bifurcation is retained until the fifth or sixth division at which time the branching appears to get out of phase.

In this study 77 specimens of *T. fagei* were examined. These were taken in plankton samples from three stations located in the Cook Inlet area of Alaska. The locations of the stations were as follows: at the mouth of Kasitsna Bay (59° 28.7′N, 151°33′W) and two stations in Tutka Bay (59°26.5′N, 151°22.7′W, and 59°25.5′N, 151°19.5′W).

The seasonal distribution of *T. fagei* was found to coincide in part with that reported for the same species parasitic on *Thysanoessa inermis* by Einarsson (1945). He found *Thalassomyces fagei* (as *Amallocystis* sp.) on mature euphausids during May only. In our work during February and March of 1963 numerous *Thysanoessa raschii* were observed, but most of the individuals taken during this time were juveniles. Early stages of *Thalassomyces fagei* first appeared on the host early in April, 1963. Mature ellobiopsids were taken from late April until about the first of June. The external structures of *T. fagei* were not present on the euphausids taken in February or March, nor were they present late in June. During May, 1963 we noted 13% average infection of *Thysanoessa raschii* by *Thalassomyces fagei.* This was based on three samples containing 239 specimens of *Thysanoessa raschii,* of which 33 were parasitized.

It appears unlikely, at least from the preserved material, that a mature *Thalassomyces fagei* could pass through the hole in the carapace of the host at molting. This is due to the fact that the host's exoskeleton closely surrounds the stalk of the ellobiopsid. Since euphausids have a high intrinsic rate of molting, one can assume either that the euphausids continue to molt with their

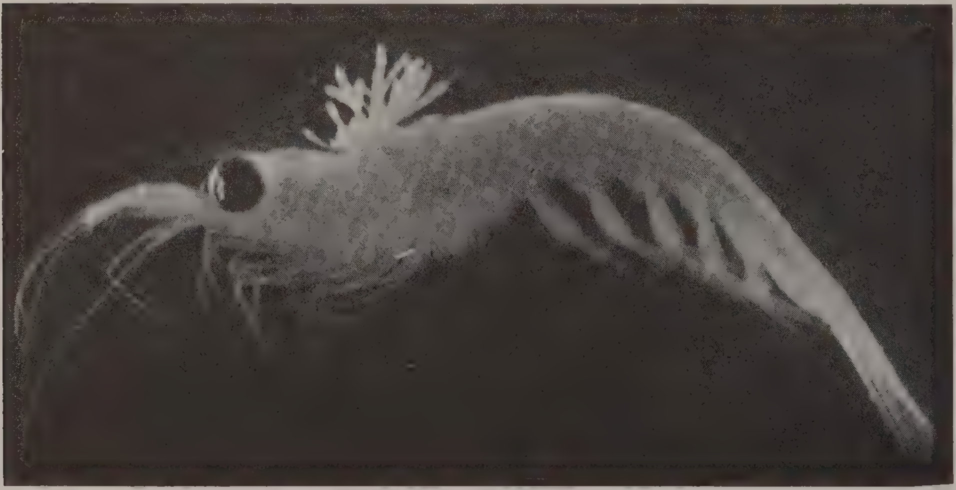

FIG. 3. Euphausid with a mature parasite.

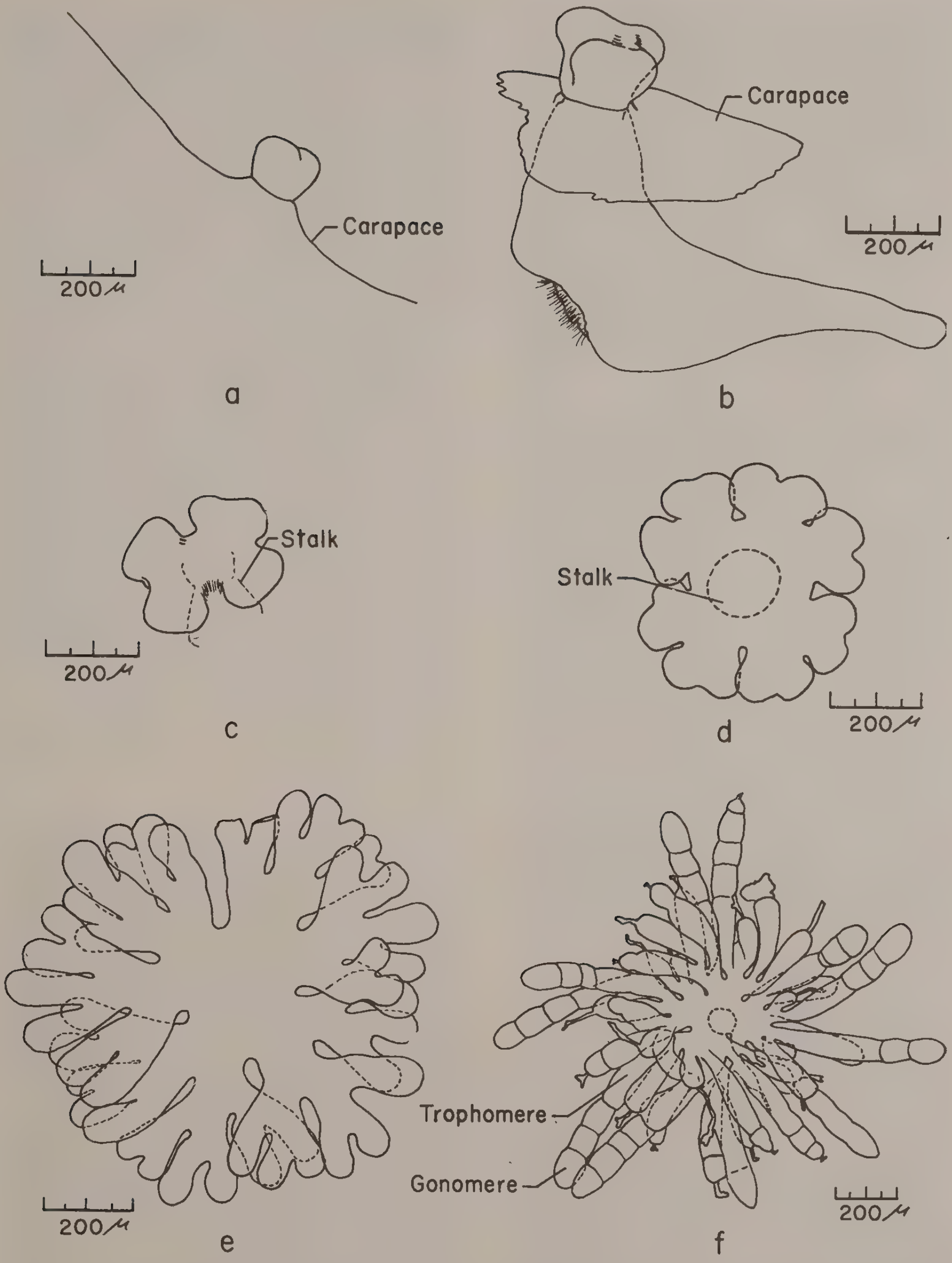
Carapace
200 μ
a
Carapace
200 μ
b
Stalk
200 μ
c
Stalk
200 μ
d
200 μ
e
Trophomere
Gonomere
200 μ
f

FIG. 4. Drawings illustrating the developmental stages of *Thalassomyces fagei*.

usual frequency or that the parasite interferes with the regulation of molting. In the former case, the external development of *T. fagei* during the intermolt would of necessity be extremely rapid. If the latter is true, as is the case with the rhizocephalans, molting would be held in abeyance while the external development and assumed reproduction of *T. fagei* take place.

In order to resolve this question and others, work on the internal development needs to be undertaken. Most studies on ellobiopsids, including this one, have dealt with the external aspects of these parasites only, while in reality it is the internal aspects which will reveal their biological status.

The observations on the effect of *Thalassomyces fagei* on *Thysanoessa raschii* agree with the reports of Einarsson (1945) on the effects of *T. fagei* on *Thysanoessa inermis*. Einarsson stated that *T. fagei* probably castrates the animal it attacks. None of the parasitized *Thysanoessa raschii* examined in this study had either the male antennal armature or the first pleopods developed as copulatory organs; in the case of females no sign of a thelycum was evident. Einarsson (1945) showed that parasitized mature females had completely disorganized ovaries through which ramifications of the stalk of the parasite extended.

Boschma (1949) sectioned parasitized euphausids and found that the ellobiopsid did not disorganize the host's ovary, although the protoplasmic excrescences which protrude through holes in the sieve plate extended throughout the organ. The ovary was not degenerated, although Boschma found that all the eggs present were small.

The most complete works on the genus *Thalassomyces* are those by Boschma (1949 and 1959), which contain a comprehensive review of the literature as well as descriptions of the species.

On the basis of these and other observations concerning the biology of ellobiopsids, a number of conclusions and hypotheses can be drawn concerning members of the genus *Thalassomyces*.

1. The development of the structures external to the euphausid and the similarity of these to reproductive structures of *Ellobiopsis* strongly suggest that they are primarily reproductive. These external structures follow the establishment of a large internal body thought to be of a vegetative nature. The length of "life" of the internal portion of the parasite and its seasonal presence are unknown. Therefore the true percentage infection cannot be determined on the basis of the external structures alone.

2. The external reproductive structures of *T. fagei* appear in early summer in Alaska, whereas they appear in midsummer in the Atlantic. The duration of this manifestation of individual ellobiopsids is unknown.

3. Our observations in this study and those of Einarsson and Boschma on the sexual development of euphausids support the interpretation that *T. fagei* suppresses the sexual development of the host. Also the ellobiopsid may interfere with the endocrine control of molting, at least during its period of external development.

4. Further understanding of the biological effects of these parasites on planktonic crustaceans will be achieved only by laboratory investigations on the internal development of the parasite and on the nature and fate of the bodies produced in the gonomere.

Thalassomyces sp.

Six specimens of *Thalassomyces* sp. were found to parasitize the mysid *Acanthomysis pseudomacropsis*. The ellobiopsid is generally located on the dorsal surface of the carapace of the mysid. In each case the mysid was parasitized by two ellobiopsids. In one instance, one of the ellobiopsids was located on the carapace, and the other was on the dorsal surface of the sixth abdominal segment of the mysid. The mature *Thalassomyces* specimens were taken in plankton samples from stations in the Kachemak Bay area of Alaska (59°27′N, 151°33′W) in October and December, 1963 and in February, 1964.

The mature parasite has 7–20 short-stalked trophomeres which are ramifications of the single central stalk. The trophomeres average 0.75 mm long, although this feature is variable. The usual number of gonomeres present on each trophomere is three, and no more than this number have been observed. The transverse diameter of the gonomeres ranges from 0.14 to 0.21 mm, the average being 0.17 mm.

The species identification of these specimens has not been determined. This ellobiopsid may be *T. fagei,* although there are differences in a number of external features of *Thalassomyces* sp. from the specimens of *T. fagei* parasitic on the euphausid *Thysanoessa raschii* taken in the same area. The number of trophomeres, the length of the trophomere stalk, and the number of gonomeres vary from the previously mentioned species. Boschma (1959) pointed out that a number of variations of this type occur among *T. fagei* individuals parasitic on different species of euphausids. The location of the ellobiopsid on the carapace tends to support the hypothesis that this is *T. fagei,* while the fact that this species parasitizes a mysid rather than a euphausid may be sufficient to propose this as a new species, inasmuch as *T. fagei* has only euphausid hosts. The only *Thalassomyces* species reported to parasitize a mysid is *T. fasciatus.* This ellobiopsid is located on the ventral side of the first abdominal segment of its host.

Until more material is available and can be examined by an authority, it is advisable to consider this ellobiopsid as *Thalassomyces* sp.

Thalassomyces capillosus

The first report of ellobiopsids from the northern and eastern Pacific was that of McCauley (1962). He found *Thalassomyces capillosus* (Fage), formerly known as *Amallocystis capillosus,* on a specimen of *Pasiphaea pacifica* Rathbun, a pelagic shrimp taken 15 miles west of Coos Bay, Oregon (43°20.4′N, 124°45.8′ W) in a midwater trawl. McCauley (1962) stated, "This work adds *P. pacifica* as a host and extends the known range of this parasite to the northeastern Pacific." According to McCauley, *T. capillosus* had previously been described as parasitic on several species of pasiphaeid shrimp, most of which were taken in the north Atlantic.

Five *Pasiphaea pacifica* taken by the Exploratory Fishing and Gear Research Base of the Bureau of Commercial Fisheries, Juneau, Alaska, were examined for ellobiopsids. A single specimen of *P. pacifica* taken by a shrimp trawl at station No. 427 located in Orca Bay, Prince William Sound, Alaska (60°34′N, 146°01′W) was parasitized. This individual was taken between depths of 74 and 120 fathoms on September 9, 1962, by Rathjen (1963). In addition, a single specimen taken in Lynn Canal in southeastern Alaska (58°51.2′ N, 135°15.5′W) was parasitized by *T. capillosus.* This pasiphaeid was taken May 14, 1964, by an Isaac-Kidd midwater trawl at a depth of 59.6 fathoms.

The ellobiopsid is located dorsal to the eyes of the host at the base of the rostrum. On one specimen there were approximately 40–50 trophomeres on either side of the rostrum; on the other specimen there were 50–60. This estimation of the number of trophomeres on the first may not be accurate because the specimen was in poor condition. Distal to the trophomere of the parasite is one or, more commonly, two gonomeres. The terminal gonomere is ovoid, almost twice as long as broad. When two gonomeres are present, the proximal one is somewhat rectangular because of the septa which separate it from the more distal gonomere and from the trophomere.

The morphology of the parasite, its size and location on the host, and the host species agree for the most part with the description of *T. capillosus* (Fage). The only discrepancy was that rather than a single gonomere there were almost always two gonomeres on each trophomere.

Effects of *T. capillosus* on the carapace of *P. pacifica* similar to those found by McCauley were noted. The rostrum is distorted and projects almost dorsad rather than anteriad. On either side of the base of the rostrum is a swelling not found in unparasitized *P. pacifica.* A dumbbell-shaped opening in the carapace extends between the two swellings. A tuft of trophomeres of *T. capillosus* extends from the tissue of the host through both of the expanded ends of the slit. Figure 5 is a camera lucida drawing illustrating the rostrum of a parasitized *P. pacifica.*

This study extends the known range of *T. capillosus* as a parasite on *Pasiphaea pacifica* from off the Oregon coast (McCauley, 1962) to the Prince William Sound area of Alaska. It is expected that further observations will fill in the range and possibly extend it still farther.

Ellobiopsis chattoni

The genus *Ellobiopsis* contains two species, *E. fagei* Hovasse and *E. chattoni* Caullery. *E. fagei* was described as parasitic on the copepod *Clausocalanus arcuicornis* Dana by Hovasse (1951). *E. chattoni* is known to be parasitic on the following copepods: *Calanus finmarchicus* (Marshall et al., 1934; Marshall and Orr, 1955; Jepps, 1937); *Calanus helgolandicus* (Boschma, 1949); *Pseudocalanus minutus* (Marshall, 1949); and *Acartia clausii* (Boschma, 1956). Marshall et al. and Marshall and Orr state that *E. chattoni* is more common on *Calanus* during the summer than the winter.

In our investigation *Metridia longa* was found to be a host for *Ellobiopsis chattoni.* This is the first record of a species of *Metridia* as host for ellobiopsids. *M. lucens,* which was present in the same samples, was not found to be parasitized by *E. chattoni.* Parasites were observed only on Stage V males and females. *M. longa* was the only copepod taken which was host to a species of ellobiopsid.

The plankton samples examined during this study were taken in southeastern Alaska at the mouth of Auke Bay (58°21′N, 134°41′W) by the Oceanography Investigation of the Bureau of Commercial Fisheries Biological Laboratory, Auke Bay, Alaska. The samples were taken monthly during 1962 and 1963. Samples were taken both during the day and at night. *Metridia longa* and *M. lucens* were the most abundant copepods in the Auke Bay samples taken during the late fall in both 1962 and 1963. Throughout the other seasons *Metridia* are taken in considerably fewer numbers. At night both species of *Metridia* are common in the sample taken just beneath the surface, whereas in the daytime *Metridia* are most common in the samples taken from approximately 20 m. Few *Metridia* were taken in the samples from Kasitsna Bay, Alaska, and none of these were parasitized by *E. chattoni.*

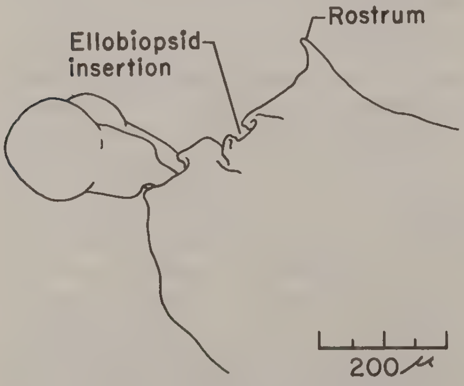

FIG. 5. Drawing showing the anterior portion of the carapace of an infected *Pasiphaea pacifica.*

E. chattoni was most abundant in the samples from Auke Bay taken in October and November of 1962 and 1963. The percentage of infection was established by examining 250 specimens of *Metridia* and calculating the percentage of infection in this subsample. Samples taken in the middle of November, 1962 showed the highest infection rate. The percentage of infected copepods ranged from 7.7% in the daytime samples to 22.4% in the nighttime samples taken at the same station. No explanation of this difference is available. During October and November, 1963 approximately 5% of the *Metridia* specimens were found to be parasitized by *E. chattoni.*

The morphology and development of *E. chattoni* is described and discussed by Jepps (1937). Our observations of *E. chattoni* on *Metridia* agree with those reported by Jepps on its parasitizing *Calanus finmarchicus.* An ellobiopsid individual initially appears as a small knoblike structure on one of the setae of any of the cephalic appendages. The mature individuals are attached by a stalk which extends into the tissue of the host's appendage. There are one or two gonomeres present on the mature ellobiopsid. The distal gonomere sometimes has an "apical cone" as described by Jepps. Although several immature *E. chattoni* may be located on a single host, no more than three mature parasites were observed on any single specimen of *M. longa.*

The finding of *Ellobiopsis chattoni* on *Metridia longa* in the coastal waters of southeastern Alaska extends the known range of this parasite from the northern Atlantic Ocean to the northeastern Pacific Ocean. This is the first report of *E. chattoni* taken in the Pacific.

ACKNOWLEDGMENTS

The authors would like to thank the following individuals whose work has aided this study:

Mr. Roland McBride, who maintains the Bureau of Commercial Fisheries Kasitsna Bay Shellfish Laboratory and is in charge of carrying out the year-round plankton sampling program; Mr. Jerrold Olson, who took the photographs; Mr. Gerald Reid, project leader for the zooplankton investigation being carried out in Auke Bay, and who allowed the use of the plankton samples taken in that area; and Miss Gail Heron and Mr. Dave Damkaer of the University of Washington Department of Oceanography, who verified the identification of the copepods.

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Increased Sensitivity to Pesticides in Sheepshead Minnows

H. T. HOLLAND, DAVID L. COPPAGE AND PHILIP A. BUTLER

Increased Sensitivity to Pesticides in Sheepshead Minnows

INTRODUCTION

Reports of resistance in fishes to various pesticides (Vinson, Boyd, and Ferguson, 1963;

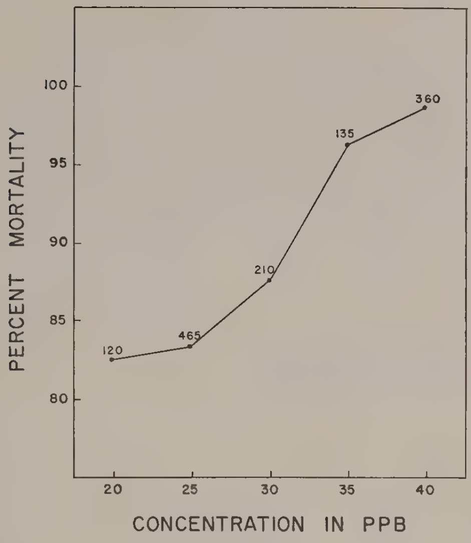

FIGURE 1.—Average percentage mortality of adult sheepshead minnows exposed to various concentrations of DDT for 24 hours. Numbers indicate sample size at each concentration.

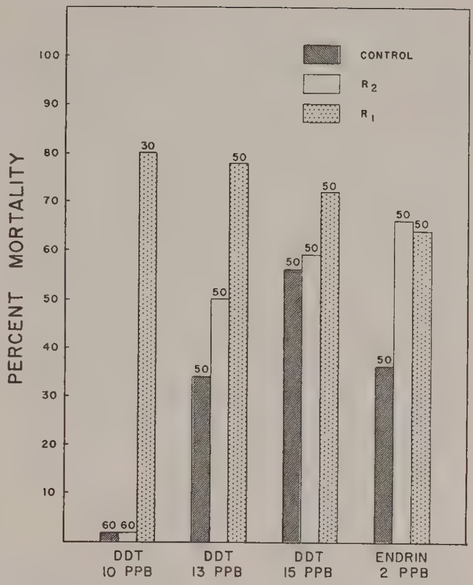

FIGURE 2.—Mortality of immature sheepshead minnows exposed for 24 hours to DDT and endrin. Number at top of each bar indicates sample size.

Ferguson et al., 1964) are based on relative toxicity data for fish collected from areas of heavy pesticide usage and fish from areas known to be free of contamination. This apparent resistance was shown to persist through several generations (Boyd and Ferguson, 1964), but the selective agent and number of generations required to produce a resistant population are unknown. The purpose of this study was to determine whether genetic resistance to pesticides in sheepshead minnows (*Cyprinodon variegatus*) could be demonstrated by testing the F_1 generation of fish surviving DDT concentrations exceeding the median tolerance limit (TL_m).

METHODS AND MATERIALS

This study was conducted at the Bureau of Commercial Fisheries Biological Laboratory, Gulf Breeze, Florida, between 13 May and 15 December 1964. Adult sheepshead minnows were seined from marsh ditches on nearby Santa Rosa Island and held in the laboratory 24 hours to eliminate weak or injured individuals. Tests were conducted in 20-liter plastic aquaria to which an acetone stock solution of the pesticide was added to give the desired concentration of toxicant. Tap water, adjusted to a salinity of 4‰ with artificial sea salt and aerated to near saturation of oxygen before testing, was used in all tests. Water temperature was 21 ± 1 C.

Aquaria were washed in detergent and water and rinsed with a 50% solution of acetone in water after termination of each test. Previous work at this laboratory utilizing C^{14} labeled DDT showed that virtually all sorbed DDT is removed from plastic by this treatment.

Brood stock was obtained as follows: five fish were placed in each of 12 to 15 aquaria (60 to 75 fish per test) containing 20 to 40 ppb (micrograms/liter) DDT for 24 hours. A total of 1,440 adult fish was tested during this study; 150 served as controls. Controls were exposed to acetone only. The number of fish tested at each concentration of DDT and percentage mortality are shown in Figure 1. No control fish died. Survivors of DDT tests in which mortality exceeded 90% were termed R_1 fish, and survivors of tests in which mortality ranged from 55 to 90% were called R_2 fish. Surviving fish were held 24 hours to provide a check on subsequent deaths, then transferred to artificial pools on Santa Rosa Island similar to the natural habitat of the species. These holding and rearing facilities consisted of five rectangular excavations in sand, approximately 15 m long, 5 m wide, and 1.25 m deep, adjacent and parallel to Santa Rosa Sound. Water depth in the pools was influenced by the tides, and varied from about 0.5 m to 1 m. Partitions of fiber glass screening and muslin cloth at the end of each pool permitted water interchange from one pool to another, but prevented fish movement. Periodically, water from the sound was allowed to pass through partitions into the pools to maintain brackish-water conditions.

The young of control and experimental fish were tested under the same conditions as described for the adults, with the exception that 10 fish were used in each aquarium. Lots of the three groups were randomly assigned to aquaria and exposed to DDT at concentrations of 10, 13, and 15 ppb and endrin at a concentration of 2 ppb.

RESISTANCE OF F_1 FISH

Reproduction of control and experimental fish in the field pools began in July. Numbers of progeny produced per fish and growth rates of their young did not differ among the three groups. Testing of the young began in the latter part of August when they averaged 30 millimeters total length; the results are shown in Figure 2.

The higher mortalities of R_1 young in all tests, as compared to control fish, were significant at the 90% level. Mortality of R_2 young was significantly greater (90% level) than the controls at a concentration of 13 ppb DDT and in the endrin.

These data indicate that a population of sheepshead minnows could tolerate an occasional heavy mortality resulting from gross pesticide pollution. The observed increased sensitivity of the F_1 generation, however, indicates that they might suffer serious mortality following relatively low levels of pesticide contamination in the environment.

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MALATHION: CHRONIC EFFECTS ON ESTUARINE FISH

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Malathion, like many of the other organic phosphorus insecticides, is toxic to fish at relatively low concentrations (Pickering, Henderson, and Lemke, 1962; Weiss, 1961), but the probability that lethal concentrations will occur throughout large bodies of estuarine water is remote. The problem is more likely to be adverse effects of sublethal concentrations of these chemicals on fish and other estuarine organisms. Published information concerning the effects of long-term exposures of fish to organic phosphorus insecticides is scant. Pickering *et al.* (1962) who reported on a 30-day exposure of fathead minnows (*Pimephales promelas*) to Delnav® found that toxicity increased with length of exposure up to 15 days, but detected no further increase during an additional 15 days. Growth rates of cutthroat trout (*Salmo clarki*) were apparently not affected by periodic exposure to malathion in feed and water (U. S. Department of the Interior, 1965). We are unaware of any publications on the chronic effects of malathion on marine fish, although it is used extensively for mosquito control in or near estuarine areas. The present study indicates that spot, *Leiostomus xanthurus,* a common sciaenid fish which spends much of its early life in the inshore waters of the Atlantic and Gulf coasts, can tolerate prolonged exposure to a sublethal concentration of malathion.

MATERIALS AND METHODS. The study was conducted at the Bureau of Commercial Fisheries Biological Laboratory, Gulf Breeze, Florida, between May and November 1965. Young-of-the-year spot were seined from local waters in February and acclimated in the laboratory 3 months before the experiment was started. We put 150 juvenile fish, averaging 39 mm in standard length, in each of two wooden tanks lined with fiberglass. The tanks—30 cm. wide, 25 cm. deep, and 244 cm. long—had a capacity of approximately 180 liters. A constant flow of 396 liters per hour of unfiltered seawater passed through each of the tanks. Fish were maintained in the tanks over a period of 26 weeks. We did not attempt to control the temperature and salinity of the seawater flowing through the tanks. Average monthly water temperatures during the experiment varied from 23° to 29° C. and average monthly salinities ranged from 2.5 percent to 2.7 percent. Fish were fed daily on a mixture of ground fish and dog food.

A stock solution of malathion[1] was metered into one of the tanks; the other served as a control. The strength of the stock solution was adjusted so that the concentration of malathion in the experimental tank was 10 ppb (micrograms/liter). This concentration was selected on the basis of results of acute-toxicity experiments. Length of exposure is critical in determining a sublethal concentration; 50 ppb malathion killed juvenile spot only after 14 days of continuous exposure. Although some of the organic phosphorus insecticides hydrolyze rather rapidly in aqueous solutions, stock solutions of malathion prepared in water of pH 7.2 remain stable for a week. Weiss and Gakstatter (1964) reported a half-life of 50 days for malathion stored in water of pH 7.0.

Fish exposed to organic phosphorus insecticides show inhibition of brain cholinesterase (ChE) levels. To determine the brain-enzyme activity during this chronic exposure, we killed five fish from each tank every 2 weeks. Following excision and wet weighing of the brain, we prepared a homogenate in phosphate buffer of pH 7.2 with a tissue concentration of 3.5 mg. per ml. One ml. of this homogenate is incubated 20 minutes at 25° C. with 1 ml. of a 0.004 M solution of acetylcholine bromide, and the residual acetylcholine (ACh) determined colorimetrically (Hestrin, 1949). Previous studies at this laboratory showed that ChE activity of the brain of spot decreases as the brain weight increases, but that variations for a particular weight are generally less than 10 percent. A line of best fit based on data from 155 unexposed specimens was considered to represent 100 percent activity for the species. Consequently, the ChE level in the brain of a fish can be expressed as percentage of normal.

Results. Neither group of fish exhibited symptoms of distress during the 26 weeks of the experiment, nor did the two lots differ significantly in growth or mortality. Brain ChE was significantly lower (90 percent level of probability) in the experimental group throughout the experiment, and appeared to stabilize at approximately 70 percent of normal. This degree of inhibition appears to have no adverse effects on these fish; we have experimentally reduced enzyme levels in spot and sheepshead minnows (*Cyprinodon variegatus*) to less than 50 percent for 48 hours without causing mortality.

Spot recover rapidly from exposure to sublethal concentrations of malathion. One week after termination of this experiment, the fish had regenerated near-normal levels of enzyme.

Immediately after termination of the chronic exposure, and again 1 week later, fish from the two groups were subjected to lethal concentrations of malathion. Differences in mortality were not significant. Brain ChE levels of the experimental fish that survived a 96-hour exposure to concentrations of 75 and 100 ppb were proportionately lower than those of control fish surviving the same concentrations.

Fish that survived the chronic exposure were subjected to a rapid drop in salinity to determine if their ability to adapt to this physiological stress was affected by malathion. We observed no differences in reactions between experimental and control groups when they were transferred directly from water with a salinity of 2.8 percent to water of salinity 1.5 percent. A gradual reduction to 0.9 percent caused distress behavior in both groups but no fish had died in 48 hours.

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[1] Furnished through the courtesy of American Cyanamid Company (*O,O*-dimethyl phosphorodithioate of diethyl mercaptosuccinate).

We observed no gross pathology of the gonads. The range of sizes of gonads in the experimental fish was similar to the range in unexposed fish of the same age group.

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The Use of Activation Analysis Methods for Tagging Post-Larval Fish

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We increased the cobalt content of post-larval flounder (genus, *Paralichthys*) to determine if the element could be detected after activation by nuclear bombardment and thus be used as a tag for these fish. When bombarded with neutrons stable cobalt is transformed to radioactive cobalt 60, which can be detected with a gamma spectrometer. A group of post-larval flounder were tagged by placing them in sea water containing stable cobalt ranging in concentration from 0.031 to 125 micrograms per milliliter. Immediately after tagging, one half of the group of tagged fish, along with control fish, were irradiated in the 10 KW reactor at North Carolina State University and then analyzed for cobalt 60 content. The remaining fish were maintained in flowing sea water for 36 days, then were irradiated and analyzed. Tagged fish in both irradiated groups had more cobalt 60 than non-tagged fish, but the difference was small, therefore a final conclusion on the usefulness of activation methods for tagging post-larval fish was not reached.

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JOHN H. HOWELL

The life cycle of the sea lamprey and a toxicological approach to its control

THE SPREAD OF THE SEA LAMPREY (*Petromyzon marinus*) into the upper Great Lakes provided a unique opportunity to evaluate the effect of a highly efficient predator in an environment where conditions were near optimum for its establishment and rapid expansion. The lamprey's destructive effect on the valuable sport and commercial fisheries of these lakes and the economic losses resulting from this destruction were sufficient to justify a program to study its natural history and develop methods to control its abundance.

The sea lamprey has affected most of the Great Lakes fisheries, but its predation on the lake trout (*Salvelinus namaycush*) inflicted the greatest damage. Prior to the appearance of the sea lamprey, annual production of lake trout from the upper Great Lakes approximated 15 million pounds—5 million from Lake Huron, 6 million from Lake Michigan, and 4 million from Lake Superior (14). Starting about 1941, production began to decline drastically. By 1961, the yield was only 300,000 pounds, of which Lakes Huron and Michigan together produced less than 1,000 pounds. The annual monetary loss to the commercial lake trout fishermen in the United States and Canada was approximately $7,350,000 (average dock price is about $0.50 per pound).

The sea lamprey was unquestionably the cause for the decline of the lake trout fishery in Lake Huron and Lake Michigan and the major cause for the decline in Lake Superior (16, 19, 20). The fish populations associated with the lake trout contained few species and consisted almost entirely of fishes on which lake trout preyed. Because no other species filled the environmental niche once occupied by the lake trout, it was reasonable to believe that the trout population could be restored if sea lamprey abundance could be controlled.

Toward the end of solving the "lamprey problem" the United States Congress, by its Act of August 18, 1949, authorized and instructed the U. S. Fish and Wildlife Service to "prosecute investigations of the abundance and distribution of sea lampreys and their effects on fishes, experiments to develop control measures, and a vigorous program for elimination and eradication of sea lamprey populations of the Great Lakes." The international character of the sea lamprey problem was formally recognized when the governments of the United States and Canada ratified a treaty on October 11, 1955. This treaty established the Great Lakes Fishery Commission and assigned to it, among other duties, the following responsibility: "To formulate and implement a comprehensive program for the purpose of eradicating or minimizing sea lamprey populations."

Attempts to control the sea lamprey required detailed knowledge of its life history and information concerning its distribution and movements during each phase of its life cycle. The magnitude of this problem can be understood better if we consider the size of the area involved. The upper three Great Lakes form a truly immense body of fresh water and one of them, Lake Superior, is the world's largest fresh-water lake. They have a combined area of 65,230 square miles and their shore lines total 7,856 miles. Their drainage area, 262,360 square miles, covers a considerable part of the midnortheast portion of the North American continent. The thousands of tributary streams range in size from intermittent brooks to major rivers and drain areas as entirely different as the relatively uninhabited shores of northern Lake Superior to the highly industrialized areas of southern Lake Huron and Lake Michigan. This size and diversity added to a problem which was considered by many to be impossible, to reduce and control, selectively, the abundance of a single species in an environment where it was well established.

The sea lamprey, the ocean form of which is anadromous, is also capable of spending its entire life cycle in fresh water. Indeed, there are native populations of sea lampreys in Lake Ontario and some of the Finger Lakes of northern New York. Until the opening of the Welland Canal in 1829, Niagara Falls prevented the landlocked lamprey of Lake Ontario from reaching the upper Great Lakes. The locks of the canal and probably Lake Erie, which has never supported a sizable lamprey population, continued to be an effective barrier since over a century elapsed before sea lampreys were first reported from the lakes above Lake Erie in 1934 (3, 23, 33). Once the lampreys reached the upper lakes, their range expanded rapidly and their numbers increased phenomenally.

Almost nothing is known concerning the life history of the anadromous sea lamprey of the Atlantic Ocean. Our knowledge of the landlocked form is much more extensive due mainly to studies by Gage (17), Surface (42), and Wigley (45) of the lamprey of Cayuga Lake in northern New York, and Applegate (3) on the natural history of the sea lamprey in Michigan waters. The following description of the life cycle is derived from these four investigators except where other sources are cited.

Mature sea lampreys (average length about 17.5 inches) must enter streams to spawn. This spawning migration takes place in April to July. To spawn successfully, the lamprey requires unidirectional water flow with velocities of 1-5 feet per second, streambed formations of gravel (¾-3 inches diameter) in riffles or patches extensive enough to permit nest building, and water temperatures of 55°F to 70°F during the spawning and hatching period.

Lampreys build nests by picking up stones with their sucker-like mouths and piling them in a horseshoe-shaped ridge with the open end facing upstream. Nesting is usually initiated by the male who is soon joined by a female. The sea lamprey is primarily monogamous, although examples of polygamous, polyandrous, and, infrequently, promiscuous spawning have been observed.

Spawning takes place in the following manner: The female anchors herself, with her oral disc, to a large stone or piece of gravel in the upstream margin of the nest. The male fastens himself to the female in the branchial region with his mouth and proceeds to wrap the posterior third of his body about that of the female so that their vents are closely approximated. The extrusion of eggs and milt is accompanied by rapid vibration of the bodies of both individuals. Spawning is repeated at 5- to 10-minute intervals until the pair is spent, usually in less than 24 hours. Lampreys die within a few days after spawning.

The fertilized eggs, which are adhesive and nonbuoyant, are carried by the current into the crescent-shaped gravel ridge. The vigorous activity accompanying successive spawning acts stirs up fine sand which is also carried downstream by the current and, when it lodges in the gravel rims, covers the eggs. Egg counts from spawning lampreys have varied from 25,000 to over 100,000, but the average is 61,500. Lamprey eggs hatch in about 13 days but further development continues in the nest approximately 7 more days. At the end of this period, the young-of-the-year larvae, which are only ¼-inch long, burrow out of the nest and are swept downstream by the relatively swift currents of the nesting area until they are carried into backwaters, eddies, or deep pools where the current is sluggish. These areas possess bottoms of silt or mixed silt and fine sand into which the young larvae burrow.

The larval sea lamprey is generally considered to be sedentary. It is obvious, however, that some movement of population takes place since they seem to be fairly evenly distributed throughout the available habitat. The major causes of larval movement are physical. Rising and falling stream levels cause periodic inundation and draining of larval habitat along the margins of streams. Flooding also causes dislocation of larval populations by disrupting the unstable bottom materials of their habitat. During high water, larval lampreys may be washed out of streams into the lakes. They are found in considerable numbers off the mouths of some streams when suitable habitat is available in the lake (19, 43, 44).

The food of larval lampreys is mainly aquatic microorganisms, particularly diatoms, which are filtered from the water taken in during respiration (15). This filtering is accomplished by branch-like papillae which spread across the entrance of the oral hood and constitute an excellent strainer to prevent large particles of undesirable matter from entering. Food particles which do enter adhere to mucal threads secreted by the larval endostyle. These mucal strands, and the adherent food particles, are drawn into the alimentary canal (31).

Estimates of the duration of the larval life of the sea lamprey have varied from four years to a maximum of seven years (40). Most of these estimates were obtained from modes in length-frequency distributions of larvae from a given population. Studies presently in progress, on larvae of known age, indicate a tremendous variation in the rate of larval growth and suggest that the duration of larval life may not be entirely a function of time. However, for purposes of presentation and to facilitate later discussion on the development of control techniques, it is assumed that the minimum length of larval life is four years.

Transformation from the larval to the parasitic stage, as reflected by external anatomical changes, begins in mid-July and extends through September. This metamorphosis adapts the animal for its free-swimming parasitic life. The U-shaped larval hood and sieve disappear. They are replaced by the tooth-lined, circular sucking disc and rasp-like tongue of the adult. Body color changes from dull brown to a bright blue-gray dorsally and a silvery-white ventrally. It is during transformation that the rudimentary eyes of the larvae appear at the surface and become functional.

After completion of metamorphosis, lampreys leave the streams and enter the lakes. The downstream migration begins in late October and is completed by early May (2, 4). Downstream movement takes place during this entire period but the greatest numbers migrate at times of high water caused by fall rains and the melting of snow in the spring.

Lampreys start their parasitic life upon entering the lakes. Our knowledge of this period, which apparently lasts from 12 to 20 months, is limited to observations on aquarium-held individuals (25, 32) and a few small-scale tagging experiments in Lake Huron (11, 35).

Parasitic lampreys held in aquaria feed only on the blood and body fluids of fishes. The attachment to the host fish is made by the tooth-lined, disc-shaped mouth and maintained by suction. The flesh of the fish is then ripped by action of the tongue until a flow of blood is started. The secretion from the buccal glands of the sea lamprey, lamphredin, has anticoagulant, hemolytic, and cytolytic properties which help to maintain and enlarge the wound (25). Fish may sometimes survive a single attack but multiple attacks are usually fatal. In the laboratory the average lamprey killed 18.5 pounds of fish during the parasitic period of its life (32). These animals, however, attained only half the weight of sea lampreys that spent their parasitic life in the lake; the destruction of fish by lake-dwelling lampreys, therefore, may be in the order of 35-40 pounds. When this figure is applied to spawning runs of as high as 25,000 individuals from a single Lake Huron tributary, the destructive potential of the sea lamprey is apparent.

The distribution of parasitic-phase lampreys in the lakes and their eventual return to the spawning streams to complete their life cycle can best be taken directly from Applegate (3), " . . . initial dispersal of recently transformed adults migrating downstream in the fall, winter, and early spring to all parts of the lake but primarily to the deeper waters; these individuals shift generally to the inshore waters during the late summer and concentrate in the bays and along the shores during the fall and early winter; here they remain until the following spring when they congregate specifically off, and in, the mouths of rivers; as the spring progresses, these sea lampreys, now mature, move into the streams to spawn and die."

The sea lamprey is most vulnerable to effective interruption of its life cycle at three stages, the two periods of migration and the relatively sedentary larval phase. Control during the parasitic stage, when the lamprey is widely dispersed throughout the enormous area of the open lakes, is considered impossible. An attack on lampreys in the vulnerable stages of life is complicated by the fact that many of the streams in which lampreys are found also contain valuable populations of sport fish and serve as spawning and nursery areas for important species of lake fishes. Therefore, methods to control the lamprey must, of necessity, be specific for it.

Control of migratory or larval populations requires first an exact knowledge of the number and location of streams in which lampreys spawn. Initial attempts to obtain these data were based on observations of migrating and spawning lampreys (3, 12, 26, 27). Later surveys have been directed toward determining the presence of larval sea lampreys and their distribution within river systems (39, 41). Starting as early as 1946 and continuing to the present, over 3,000 tributaries to the three upper Great Lakes have been surveyed to determine if they are used by sea lampreys. If lampreys were found in all these streams, control would be impractical. Fortunately, the highly specific, though not fully understood, habitat requirements of the lamprey during spawning and larval life limit it to 305 streams.

Initial attempts at control were directed toward the migratory stages. Destruction of newly transformed lampreys during their downstream migration would have been most desirable since each generation could have been removed before it parasitized fish. Mechanical barriers and screens were developed to take these migrants but proved difficult or impossible to maintain, especially during spring floods when the heaviest downstream migration of lampreys occurred. Electrocution of young lampreys was difficult and did not succeed well enough to justify the enormous cost of electrical energy.

Blocking and capturing of spawning runs proved to be more practical. Electrical barriers and traps were developed, tested, and found to be economically feasible (13, 28, 29). This method of control nevertheless has some serious disadvantages. Effects in terms of reduced predation are delayed for five years since at least four generations of larvae present in streams and one parasitic generation in the lake had to complete or pass through the parasitic stage. Spawning migrations of sea lampreys occur over a period of approximately four months during the spring. This period is marked by extreme fluctuations in stream flow that make it difficult to maintain a "lamprey-tight" block during floods. The reproductive potential of the sea lamprey is so great that "minor" escapement to the spawning grounds can be sufficient to maintain the population at an undesirably high level.

Although the disadvantages of blocking spawning runs were recognized, it was decided in the spring of 1953 to initiate experimental control in the Lake Superior basin by this method (30) while continuing a search for techniques which would be more effective. Eventually 68 lamprey-spawning streams tributary to Lake Superior were blocked. This barrier system was later supplanted by another control method but it provided extremely valuable information on lamprey abundance. Counts of upstream migrants at 22 index barriers continue to offer the most reliable measure of population abundance.

The larval stage was considered initially to be the least promising of the three possible points of attack on the sea lamprey. Larval lampreys are widely distributed throughout streams where they are present and are closely associated with valuable sport fishes. These disadvantages are balanced by having all larval generations subject to destruction at one time. Also, destruction of larval populations prevents lampreys from reaching the parasitic stage. Once control is established it can be maintained on a periodic basis since any new generations will not become parasitic for at least four years. Because of these obvious advantages it was decided to attempt to attack the larval stage with selective toxicants.

The use of general toxicants to control fish is well known in fishery management. Considerable time and effort have been expended on the development of chemicals for the eradication of entire fish populations from lakes and streams. Among the toxicants have been materials such as cube and derris root, rotenone, cresol, copper sulphate, and toxaphene. As fishery workers became more knowledgeable in the application of general poisons, attempts were made to use them for the selective kill of one species. This use of indiscriminately toxic materials has been of necessity confined to those species which tend to concentrate in a separate part of the aquatic environment at some time in their life cycle. A truly selective material to destroy larval lampreys must be toxic only to larval lampreys over a wide enough range of concentration to allow its use when other species are present in the same environment.

To locate such materials a program of "screening" was initiated on a large and diverse series of predominantly organic chemicals. The screening procedures were designed to identify chemicals acutely toxic to sea lampreys at extremely low concentrations and nontoxic to other species at the same concentrations.

Over 4,000 chemicals were "screened" in 1953-57 (7). Only two displayed a degree of selectivity that was considered sufficient to justify additional study. One of them, O-ethyl-S-pentachlorophenylthiocarbonate (6), proved to be so difficult to formulate, apply, and analyze that it was soon dropped from the program. The second material, 3-bromo-4-nitrophenol (5) was expensive and difficult to synthesize, but the testing of other halo-nitrophenols resulted in the discovery of related chemicals which were selectively toxic to larval lampreys (9). Among these compounds, 3-trifluoromethyl-4-nitrophenol (TFM) met the requirements for application and became the chemical of choice (8).

The procedures for applying TFM were developed during a series of experimental stream treatments (8). Numerous factors must be controlled and monitored with precision during the application of TFM. This chemical is ineffective if the concentration is too low, or indiscriminately toxic if the concentration is too high. The direct application of a chemical to all areas of a stream requiring treatment is impossible, but the downstream movement of water provides the necessary distribution if a water-soluble material such as TFM is applied upstream from all areas inhabited by larval lampreys. The introduction of TFM at a constant rate over a period of time produces a "bank" or "block" of treated water which retains its identity as it moves downstream. It is possible to create a flow of sufficient concentration over enough time to kill lamprey larvae but not other stream organisms. Analysis of periodic samples from the treated water indicates changes taking place as it moves downstream. The concentration or length of time can be increased, if necessary, by a supplemental application of chemical.

Proportioning devices were developed which delivered accurate volumes of a liquid formulation of TFM (1), and colorimetric-analysis techniques were devised which were suitable for field use (36, 37). It was recognized during laboratory studies on the toxicity of TFM that the quality of the dilution water affected its biological activity (8). To permit adjustment for this variation in toxicity, mobile bioassay laboratories were built for determining the toxicity and selectivity of TFM in each stream immediately prior to treatment (22, 24).

Chemical treatment of Lake Superior tributaries containing larval lampreys began in the fall of 1958 and was completed by the fall of 1960. The results of these treatments were most dramatically demonstrated by their effect on the population of spawning migrants. The catch of migrating spawners in 22 index barriers on the United States shore of Lake Superior in 1961 was 67,230. In 1962, the first year when the effect of chemical treatments could be expected to appear, the number of lampreys in the spawning run was 9,127, a reduction of 86.4%. The 1963 and 1964 catches were

11,111 and 11,961, respectively. The 1964 catch was still 82.2% less than the 1961 catch. The second round of treatments, now in progress in Lake Superior tributaries, should further reduce the lamprey population.

Field experience with TFM in sea lamprey control confirmed observations on the selectivity of the material which had been made in the laboratory (10, 34) and during experimental stream treatments (8). Almost complete kills of larval sea lampreys were attained. Larval lampreys of the genera *Lampetra* and *Ichthyomyzon* were also destroyed. Fishes from the following families were the most resistant to the toxic effects of TFM: Acipenseridae (sturgeons), Lepisosteidae (gars), Clupeidae (herrings), Salmonidae (salmon and trout), Osmeridae (smelts), Coregonidae (whitefishes), Cyprinidae (minnows), Gasterosteidae (sticklebacks), and Centrarchidae (sunfishes). Some members of the following families suffered mortalities during individual treatments: Ameiuridae (catfishes), Cyprinodontidae (killifishes), Esocidae (pikes), Catostomidae (suckers), Aphredoderidae (pirate perches), Cottidae (sculpins), and Percidae (perches). The families Amiidae (bowfin), Gadidae (cods), Umbridae (mudminnows), and Percopsidae (trout-perches) were usually killed but the level of mortality was less than that for the larval lamprey. Other aquatic vertebrates are unaffected by TFM with the exception of *Necturus maculosus*, which seems to be as susceptible as lampreys.

The effect of toxic substances on invertebrates is extremely difficult to evaluate under field conditions. Laboratory studies have indicated that the levels of TFM used in stream treatments are generally nontoxic to invertebrates with a few notable exceptions (34). Among the aquatic stages of insects, larvae of the burrowing mayflies (Ephemeridae) and the blackflies (Simuliidae) are highly susceptible. Fresh-water Hydrozoa and Turbellaria also are sensitive to TFM. The concentrations of TFM used for sea lamprey control do not appear to have molluscicidal, algaicidal, or herbicidal properties.

Toxicity tests with TFM have been conducted on rats, rabbits, dogs, cows, and whitetail deer. Results of studies of both acute and chronic toxicity have been negative when the animals were exposed at levels comparable to those obtained from drinking stream water during a chemical treatment.

Even though a reduction of 80-85% in the numbers of lampreys in Lake Superior was less than hoped for and below that which ultimately may be attained, indications are strong that the lake trout are responding to the reduction in lamprey predation. The incidence of fresh lamprey wounds has been declining steadily since the completion of the first round of treatments. The survival and hence the average size of lake trout has been increasing. Spawning fish are present in Lake Superior in considerable numbers for the first time since 1959.

The search for more efficient larvicides for the sea lamprey is continuing. Recently it was discovered that over 50 salicylanilides were highly toxic and selective for larval lampreys (38). Some of the salicylanilides can be used to form synergistic mixtures with TFM. The addition of only 2% of the compound, 5,2′-dichloro-4′-nitrosalicylanilide to TFM more than doubles toxicity without seriously affecting selectivity (21). Applications of this mixture have had considerable success in the soft-water streams on the north shore of Lake Superior.

Selective toxicants are not new. The rapidly expanding fields of pharmacology and chemotherapy could not exist without them. In recent years the botanist has had considerable success with compounds such as 2,4-D for the selective control of broadleaf plants. The entomologist's reliance on broad-spectrum toxicants such as DDT and the organophosphates is being replaced by interest in more selective control. Systemic insecticides offer a good example. Veterinary parasitologists are now using antiparasitic compounds which are selective enough to be administered continuously as preventives rather than therapeutic agents. Except for chemotherapeutic agents directed toward specific organs within an animal or plant, selective toxicants generally have selected between diverse groups—plant and insect, and vertebrate and invertebrate. The use of selective toxicants to control the sea lamprey is the first practical demonstration of separation of vertebrate from vertebrate.

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Procedure for Analysis of Schooling Behavior[1]

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ABSTRACT

A method for the analysis of schooling behavior applicable to field and laboratory studies is presented. Three indices were developed to measure the behavior of a school, from motion pictures. Two of the indices are measures of the distance among individuals in a school, and the other is a measure of the differences in orientation among the individuals. A value for each index was calculated for each motion-picture frame analyzed. A coordinate reader and digitizer used to analyze films permitted the operator to record automatically on IBM cards the X and Y coordinates for the positions of the head and tail of each fish in a frame. A computer program was written to calculate the three indices from the coordinates, to convert the measurements to actual distance, and to make statistical comparisons.

Laboratory experiment on the influence of food deprivation on schooling behavior of juvenile jack mackerel, *Trachurus symmetricus* (Ayres) indicated: schools became compact immediately after feeding; the intervals among fish expanded during a deprivation period; and differences in orientation were related to the size of the individuals.

A PROCEDURE was needed to express quantitatively the behavior of schools of fish. The method needed to be suitable for both field and laboratory studies and had to be adapted to the schooling habits of fast-swimming pelagic fishes. This paper describes a procedure that has these attributes. To illustrate the functioning of this technique, laboratory data are presented on the effect of feeding and food deprivation on the behavior of schools of juveniles of jack mackerel, *Trachurus symmetricus* (Ayres).

Procedures previously used to quantify schooling behavior were designed for laboratory studies and would be difficult to appy in the field. They include: ranked estimates of the degree of aggregation (Bowen, 1931); measurements from photographs of the distance between two parallel fish in a school (Breder, 1954); density measurements based on visual approximation of the position of fish against vertical and horizontal grids (Keenleyside, 1955); calculations of swimming speeds from cinematographic data (Steven, 1959); and the perimeter of the smallest polygon which encloses a school (Williams, 1964). John (1964) developed an index of schooling based on the assignment of a rank to each possible horizontal grouping of six fish. If only two of the fish were near each other, the value 1 was used; if all fish were together, the value 10 was used; and intermediate groupings were assigned ranks between 1 and 10.

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No consensus exists on the essential characteristics of a school. Breder and Halpern (1946) considered the term to include aggregations of fish in which the spacing and orientation of the individuals are uniform. Keenleyside (1955) used a broader definition. He considered a school to be "an aggregation formed when one fish reacts to one or more other fish by staying near them." The jack mackerel is a schooling fish by either definition.

METHODS

APPARATUS

Experiments were conducted in a light-tight chamber, 2.4 m wide, 3 m long, and 2.4 m high. The inside walls, ceiling, and all structures inside the chamber were painted flat white. A laminated plywood tank was constructed with the top in the same proportions as a 16-mm motion-picture frame. The tank was 141 cm long, 110 cm wide, and 27 cm deep. The inside of the tank was coated with white-pigmented resin and two black cross lines, for aligning the camera, were drawn on the bottom. The water in the tank was 18 cm deep and was recirculated.

A 16-mm movie camera was mounted inside a light-tight hatch on the outside of the chamber, 71 cm above the tank. The lens of the camera projected through a port, 11 cm in diameter, in the ceiling of the chamber directly over the center of the tank. The camera was driven by a synchronous motor and controlled by an interval timer.

The chamber was illuminated by eight 100-w, 2850° Kelvin, clear tungsten lamps spaced at equal intervals around the perimeter of the tank. The tops of the lamps were 2 cm below the upper edge of the tank wall. Since the tank walls were opaque, the only light entering the water was that reflected from the sides and ceiling of the chamber. The light in the tank was distributed relatively uniformly.

An electric clock with numerated cams for hours, minutes, and seconds, mounted on the outside edge of the tank appeared in every frame of the film. All experiments were conducted in a temporary laboratory that had a closed seawater system. A thermograph recorded the water temperature, which was 22 ± 2 C. Six juvenile jack mackerel were used in each experimental group — the same number used in certain other studies of schooling behavior (Keenleyside, 1955; John, 1964).

THREE INDICES OF SCHOOLING

Three indices were developed to measure schooling behavior from time-lapse photographs of schools in the horizontal plane. Two — mean separation distance and mean distance to the nearest neighbor — are measurements of the compactness of the school, and one — mean angular deviation — is a measure of the differences in orientation among individuals in the school. All measurements are in millimeters. Mean distance to the nearest neighbor is a modification of a statistic used in plant ecology studies (Clark and Evans, 1954); the other two indices are new.

The *mean separation distance* is the average of the horizontal distances separating each fish from every other fish in the school. The distance from the head of one fish to the head of every other fish in the school is measured. These measurements are made for each fish in the school, except no measurement is duplicated. Thus, for a school of six fish, the mean of 15 measurements is designated the mean separation distance.

Mean distance to the nearest neighbor is the average of the distances from each fish in a school to its nearest neighbor. The measurement is made between the two closest points on the midline of the bodies of the two fish, regardless of their orientation. The same measurement is used twice if two individuals are closer to each other than to any other individual in the school.

The *mean angular deviation* is a measure of the differences in orientation among fish within a school. To calculate the index, the heading of each fish, in degrees, is determined. Then the resultant direction of the school is computed by assigning each fish a value of one and adding the headings vectorially. The number of degrees each fish deviates from the resultant direction of the school is determined and a mean calculated. This value is the mean angular deviation.

The values for mean angular deviation ranged from near 0 (for schools of uniformly oriented fish) to about 90° (for groups composed of randomly oriented individuals).

The three indices were calculated for each photograph of a school.

Films were analyzed by use of a coordinate reader and digitizer[2] to decrease data-processing time. To analyze a single photograph of six fish by hand with single-frame analyst projector required 30 min, but less than 30 sec were needed when a coordinate reader was used. The reader operated as follows: film was projected on a ground-glass screen; the operator, by turning two controls, moved an X and Y crossline across the glass screen; and the position of each coordinate was recorded on an IBM card by depressing a foot pedal. In this manner, the X and Y coordinates for the tip of the snout and the tail of each fish in a frame were recorded. A computer program[3] was written to calculate, from the coordinates, the three indices for each frame, to convert the reader units into the actual distance in millimeters, and to make statistical comparisons of groups of 25 indices (Mann-Whitney *U* test — Siegel, 1956).

One unit on the screen equaled 0.37 mm in the tank. The coordinates for the position of the snout and tail of the fish were measured with a precision of ±4 reader units. Thus, the actual distance between fish was measured with a precision of ±1.5 mm.

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[2] These are semi-automatic record-reading machines designed to analyze data recorded as images or traces on transparent, translucent, or opaque film or paper. Several models are available from manufacturers.

[3] Available in Fortran-63 program decks. Copies may be obtained from the U.S. Bureau of Commercial Fisheries Tuna Resources Laboratory, La Jolla, California.

Analysis of a Continuous Film

Groups of juvenile jack mackerel were almost continually in motion. The swimming speed of a group was not constant but varied from 7 to 15 cm/sec. The schools did not mill or show any habitual sequence of maneuvers. Groups appeared to make random passages in all areas of the tank with equal frequency.

Each frame of a continuous sequence was analyzed to determine the sensitivity of the three indices to minor changes in the dynamics of the school. Figure 1 shows the changes in each index for a school of six jack mackerel during a 100-frame sequence taken at a speed of 12 frames/sec. During this period, the school executed three turns; the first was the sharpest and the last the most gradual (Fig. 2). The three peaks in mean angular deviation shown in Fig. 1 correspond with the three turns; the more acute the turn, the greater was the oscillation in the mean angular deviation.

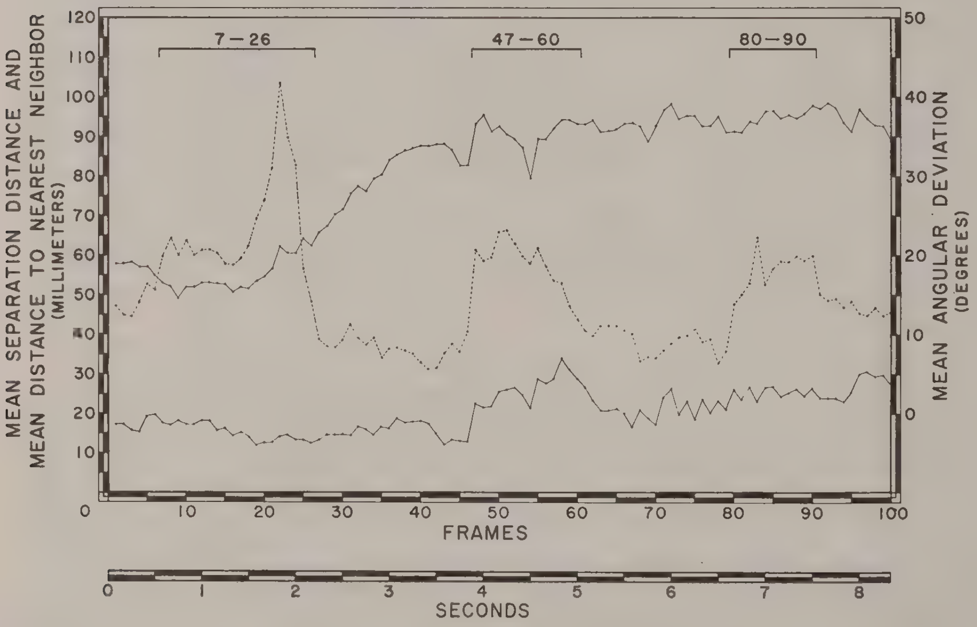


Fig. 1. Mean separation distances (upper, solid line), mean distance to nearest neighbor (lower, solid line), and mean angular deviation (middle, broken line) of a school of six jack mackerel for 100 continuous frames taken at 12 frames/sec. Brackets indicate the three major oscillations in angular deviation.

The school was relatively compact prior to the first turn but lengthened after turning; the fish became arranged in an overlaping file 4–5 fish long. During the second turn the school shortened and widened; the fish became distributed in 2 or 3 ranks of 1–3 fish each. The school retained this form during the remainder of the sequence. Both indices of spacing became higher in response to this general decrease in compactness. As the school elongated

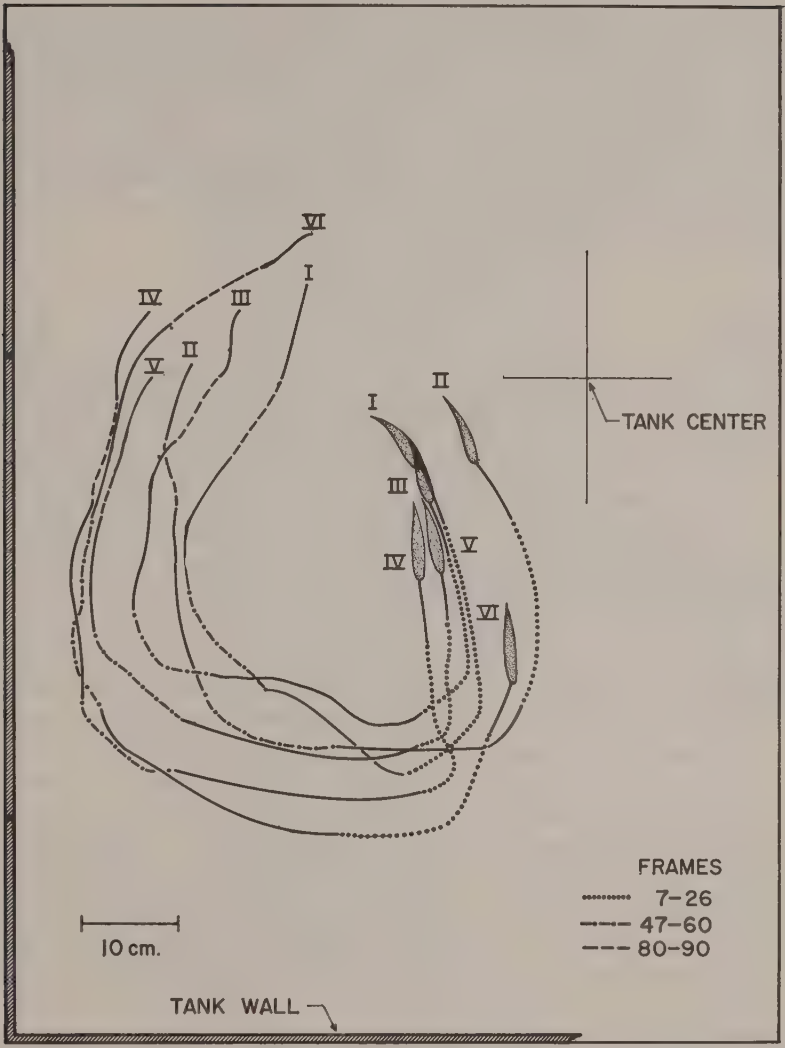


FIG. 2. Movements of the school of six jack mackerel during the 100-frame sequence shown in Fig. 1. Positions of the fish in the first frame are drawn. Subsequent positions are indicated by lines. The three groups of broken lines indicate the three major oscillations in angular deviation. (Roman numerals identify individual fish.) Movements were charted by projecting each of the 100 frames in sequence and plotting the position of each fish in every frame.

(frames 26–47) separation distance increased rapidly; distance to nearest neighbor, on the other hand, did not change. At the start of the second turn (frame 47) distance to the nearest neighbor increased sharply but separation distance, already high, increased only slightly.

Analysis of continuous film demonstrated that the indices were sensitive to minor changes in the activities of a school. If the period under study was minutes or hours rather than seconds, analysis of every frame in a continuous series was impractical. If single photographs were taken at intervals of 1 min or longer, an observation could fall at any point in the graph shown in Fig. 1. Thus, the angular deviation for such a point could be as high as 43° or as low as 6°. Similar variability would be encountered in the mean separation distance and distance to nearest neighbor. Thus, if intermittent observations are used, considerable oscillation can be expected between points and only major changes in behavior can be evaluated.

FOOD DEPRIVATION

PROCEDURES

To determine the effect of feeding and food deprivation on the spacing and alignment of juvenile jack mackerel, three groups of six fish of three different sizes were used. The mean standard length of each group was: group A, 69 mm; group B, 84 mm; and group C, 106 mm. The fish were fed frozen brine shrimp by lowering the food through the camera port. Groups A and B received 10 g per feeding, and group C, 15 g per feeding. The size of the rations was determined during previous feeding periods and was the amount of food required by each group to reach satiation. Schools were photographed at 1-min intervals for 54 hr. The fish were fed twice during the period: once at the end of a 24-hr deprivation period, and again at the end of a 48-hr deprivation period.

Each group was placed in the experimental tank at 1500 hr, 2 days prior to the initiation of the experiment. At 1100 hr the following day the group was fed. Filming began 22 hr later, at 0900 hr; 2 hr later the fish were fed. They were not fed again for 48 hr; photography was terminated 4 hr after the last feeding. From the time the fish were placed in the tank until filming began, the fish experienced normal daylight, as the chamber was illuminated by the sunlight that passed through the open door. When photography started, the lights in the chamber were turned on, and the door was closed. The door remained closed and the fish were under constant illumination until the experiment ended 54 hr later.

DATA ANALYSIS

In each experiment every frame was analyzed for the 50 min before each feeding and for the 150 min after food was introduced. The 200 values for each of the indices were grouped separately, for statistical comparison, into 8 sets of 25 values each. Sets 1 and 2 occurred before feeding and sets 3 through 8 after food was added. This arrangement allowed a detailed analysis of the change in schooling behavior associated with feeding. The data are presented in their original form for group C; for groups A and B only the results of the statistical comparisons are shown.

The Mann-Whitney *U* test was used to make all statistical comparisons. Although this nonparametric test functioned well in this application, its selection was more or less arbitrary. Undoubtedly, other tests could be used with equal effectiveness.

Separation Distance and Distance to Nearest Neighbor

Schools of jack mackerel were more compact during and after feeding than before they were fed (Fig. 3–6; Table I).

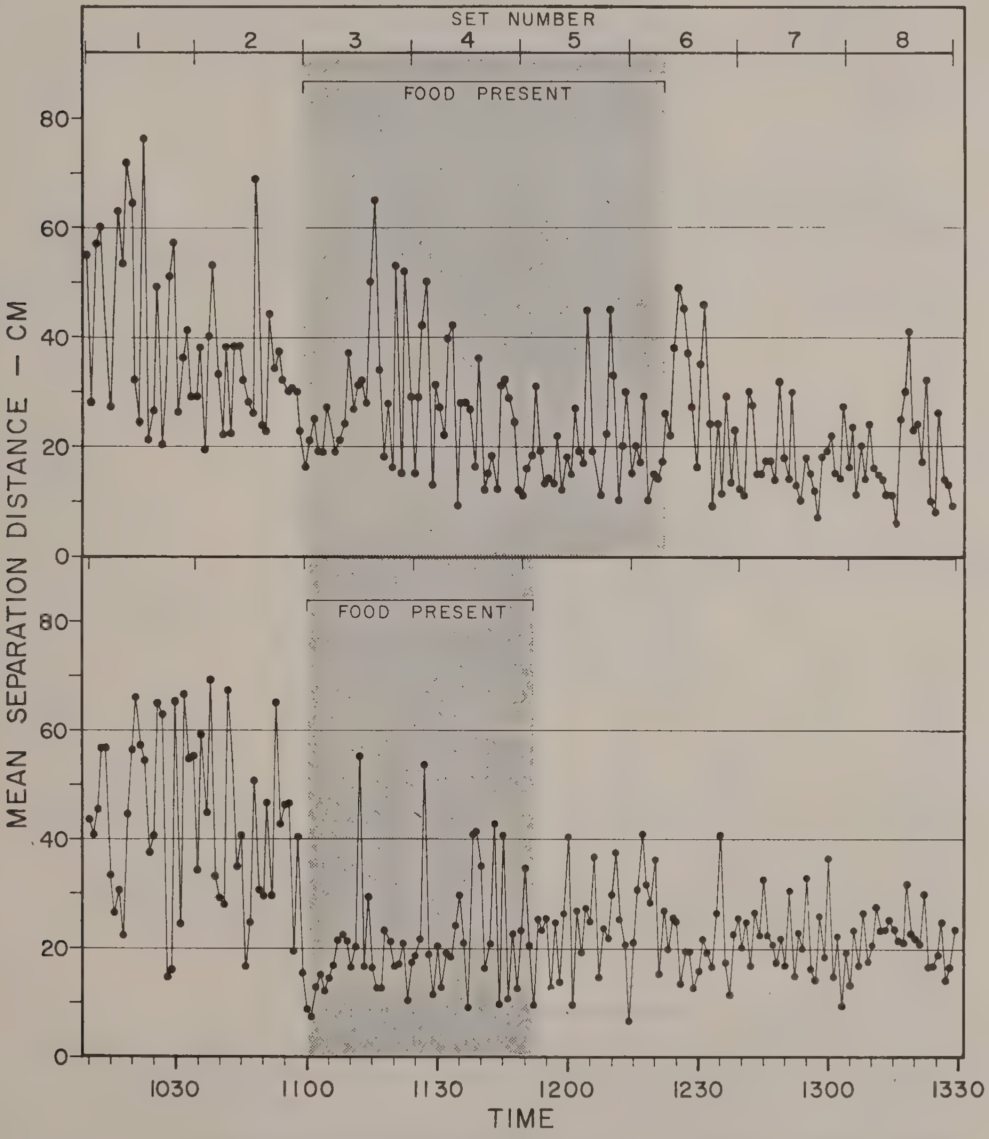


FIG. 3. *Top.* Mean separation distances of a school of six jack mackerel (group C) recorded at 1-min intervals during and after a 24 hr food-deprivation period. Shaded area represents period food was present. One-minute intervals are divided into eight groups of 25 observations each for the statistical comparison shown in Table I.

FIG. 4. *Bottom.* Mean separation distances of a school of six jack mackerel (group C) recorded at 1-min intervals during and after a 48-hr food-deprivation period. Shaded area represents period food was present. One-minute intervals are divided into eight groups of 25 observations each for the statistical comparison shown in Table I.

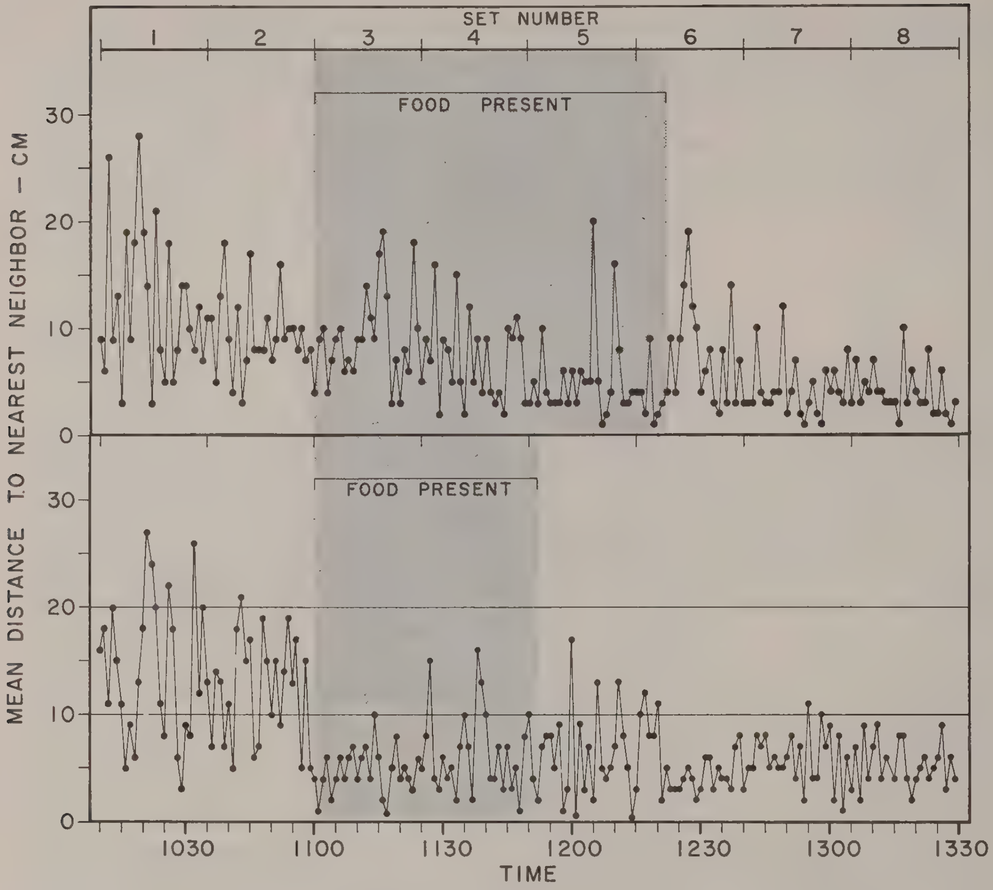


FIG. 5. *Top.* Mean distances to nearest neighbor of a school of six jack mackerel (group C) recorded at 1-min intervals during and after a 24-hr food-deprivation period. Shaded area represents period food was present. One-minute intervals are divided into eight groups of 25 observations each for the statistical comparison shown in Table I.

FIG. 6. *Bottom.* Mean distances to nearest neighbor of a school of six jack mackerel (group C) recorded at 1-min intervals during and after a 48-hr food-deprivation period. Shaded area represents period food was present. One-minute intervals are divided into eight groups of 25 observations each for the statistical comparison shown in Table I.

The difference in mean separation distance between the two sets prior to feeding was not significant (Table I, sets 1 and 2). Differences were significant between set 1 and those after food was introduced (sets 3–8). During the first 25 min of the feeding period (Fig. 3–6, set 3) the food was concentrated in one area and frequently the fish were aggregated near the food. The food became dispersed thereafter and the spacing of the fish within the school was more directly a reflection of their behavior rather than the distribution of the food.

In group A, after 24 hr of deprivation, not all of the sets of observations after the introduction of food were different from set 1; after the 48-hr deprivation period, all of these sets (3–8) were different from set 1. Greater differences

TABLE I. *z* values[a] obtained from statistical comparisons of three indices of schooling behavior for three jack mackerel schools; set 1 (before feeding) is compared to set 2 (before feeding) and sets 3–8 (during and after feeding). (Values for which $p > 0.05$ are indicated by ns.)

Relation to time of feeding	Values of set 1 compared with those of set:	Fed after 24 hr deprivation			Fed after 48 hr deprivation		
		A	B	C	A	B	C
		Separation distance					
Before	2	1.43 ns.	0.01 ns.	1.91 ns.	0.92 ns.	0.46 ns.	1.19 ns.
During	3	5.77	5.25	3.11	4.96	5.85	5.05
During	4	2.59	3.75	3.41	3.29	4.26	4.36
During or after[b]	5	1.29 ns.	4.22	4.74	4.59	4.41	4.47
During or after	6	2.45	3.09	4.03	5.56	3.87	4.47
After	7	1.29 ns.	3.68	5.27	5.09	4.34	4.80
After	8	0.55 ns.	3.29	5.17	5.15	4.55	4.76
		Distance to nearest neighbor					
Before	2	1.85 ns.	2.03	1.25 ns.	0.84 ns.	0.94 ns.	0.88 ns.
During	3	5.93	5.00	1.48 ns.	4.32	5.19	5.15
During	4	3.52	4.10	2.76	1.93 ns.	3.81	4.24
During or after[b]	5	2.20	2.76	4.34	3.54	3.48	4.20
During or after	6	3.29	2.34	3.15	5.42	3.44	4.78
After	7	1.33 ns.	3.35	4.78	5.09	3.52	4.61
After	8	1.70 ns.	2.20	5.00	3.95	3.68	4.92
		Angular deviation					
Before	2	0.28 ns.	0.36 ns.	1.29 ns.	0.03 ns.	0.40 ns.	0.03 ns.
During	3	2.32	2.44	3.93	2.28	1.70 ns.	1.31 ns.
During	4	0.57 ns.	2.40	1.41 ns.	0.69 ns.	2.82	0.55 ns.
During or after[b]	5	1.14 ns.	2.67	1.06 ns.	4.34	1.48 ns.	1.66 ns.
During or after	6	0.69 ns.	2.98	0.15 ns.	4.86	2.36	2.28
After	7	1.15 ns.	2.82	0.20 ns.	4.90	1.19 ns.	3.72
After	8	0.24 ns.	2.32	1.25 ns.	5.07	1.29 ns.	3.62

[a] Test criterion of Mann-Whitney *U* test.

[b] Time required for each school to consume all food varied. For all groups, the food was consumed by the end of set 6.

were obtained in the 48-hr test because the fish were spaced more widely before they were fed. The mean separation distance immediately after feeding was the same regardless of the length of the preceding deprivation period.

The schools became more compact during the time that would have been the first hours of darkness if the fish had not been kept under constant illumination (Fig. 7). A possible explanation is that prior to the experiment the fish may have responded to lower levels of illumination by swimming closer together, and this behavior persisted under constant illumination.

The times at which the fish were fed are represented by the second and penultimate points in Fig. 7. These points were lower than the preceding points, as would be expected from the analysis of the data presented above.

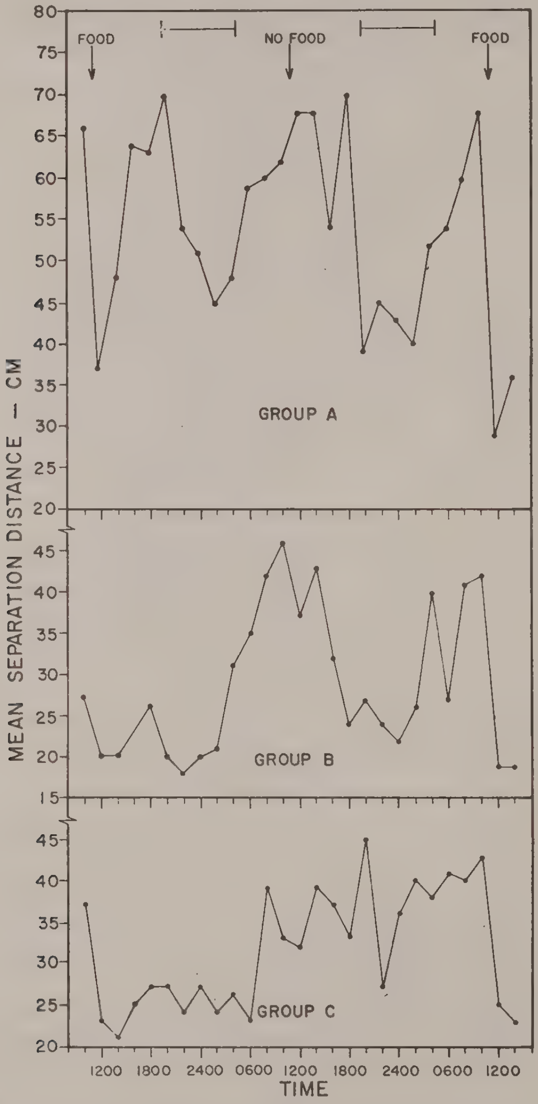


FIG. 7. Mean separation distances for three groups of six jack mackerel during a 54-hr period under constant illumination. Each point represents 2 hr and is an average of 12 individually calculated mean separation distances. Time scale indicates midpoint of each 2-hr period. Horizontal bars near top of upper panel represent the period each day that fish were in the dark prior to filming. Fish were fed at 1100 hr on the first and third day of the experiment.

Mean distance to nearest neighbor (Fig. 5, 6; Table I) showed the same changes during and after feeding as did mean separation distance. Distance to nearest neighbor also decreased during the first hours of darkness as described above for separation distance. A graph of these data was not included because of the close resemblance to that of separation distance.

Angular Deviation

The mean angular deviation of schools changed during feeding. In the initial stage of feeding (set 3) the fish fed continually and independently. This behavior caused an increase in the mean angular deviation (Fig. 8; Table I). After approximately 25 min the school re-formed. Thereafter, fish left the school briefly to feed until all food was consumed. A fish that left the school, executed a short charge, captured a brine shrimp, and returned.

Toward the end of the 48-hr deprivation period, groups B and C showed as great differences in orientation as they did during the initial stage of feeding. The angular deviation for these two groups did not increase during the first 25 min of the second feeding period but remained at the same level (Fig. 8, 9).

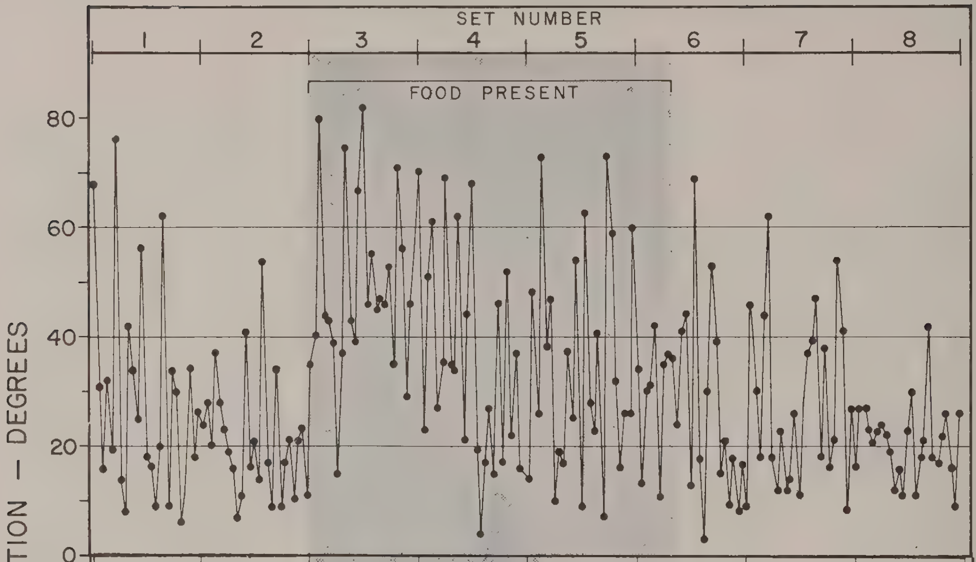
The three groups (Fig. 10) showed different levels of angular deviation during the 54-hr experimental period; the angular deviation of the school was related to the size of the fish. Group A, composed of the smallest fish, was the least oriented school; group C, composed of the largest fish, showed the least differences in orientation. Group B was intermediate in both fish length and orientation of the school. Tests based on all points shown in Fig. 10 demonstrated that the differences between each group and every other group were significant at the 0.001 probability level or lower.

The smaller differences in orientation of the larger juveniles probably was not an artifact related to the size of the tank. If the size of the tank had influenced the results, the larger fish would have been more disorganized because, owing to their size, they were forced to turn more frequently than were smaller fish.

Differences in behavior between the fish composing group A and the larger fish of groups B and C were noted at the time the fish were captured. All fish were caught at night beneath a lamp. Fish of the size of those in group A swam beneath the light individually; larger individuals, as those in groups B and C, swam beneath the light in a school. Nevertheless, fish of group A schooled in the laboratory although they were usually more widely spaced (Fig. 7) and showed greater differences in orientation than did the larger fish.

EVALUATION OF INDICES

Mean separation distance and mean distance to nearest neighbor are measurements of the relative compactness of schools but the information they provide is not identical. Separation distance is an average of all spatial relationships among fish in a school, whereas distance to nearest neighbor is an average of only the one relationship. Distance to nearest neighbor cannot distinguish between a school whose individuals are congregated in one spot from a school consisting of scattered groupings of individuals (Clark and Evans, 1954). A plot of separation distance against distance to nearest neighbor shows



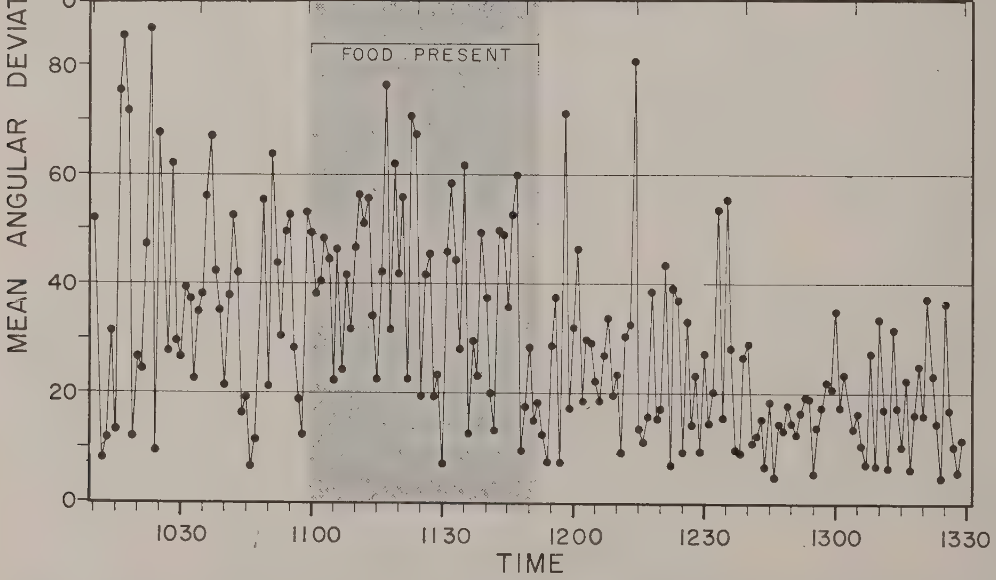


FIG. 8. *Top.* Mean angular deviations of a school of six jack mackerel (group C) recorded at 1-min intervals during and after a 24-hr food-deprivation period. Shaded area represents period food was present. One-minute intervals are divided into eight groups of 25 observations each for the statistical comparison shown in Table I.

FIG. 9. *Bottom.* Mean angular deviations of a school of six jack mackerel (group C) recorded at 1-min intervals during and after a 48-hr food-deprivation period. Shaded area represents period food was present. One-minute intervals are divided into eight groups of 25 observations each for the statistical comparison shown in Table I.

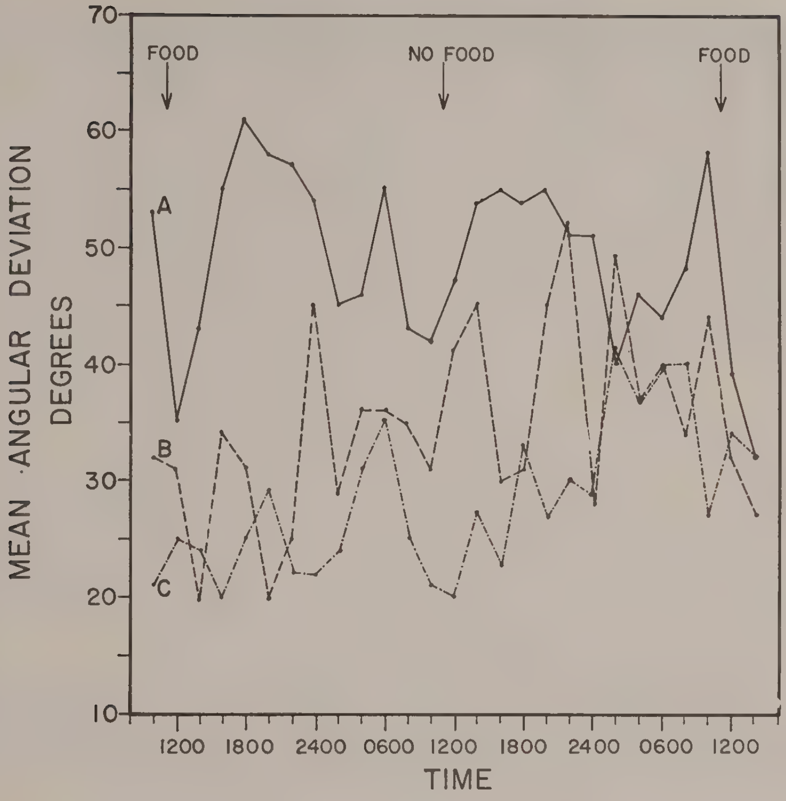


FIG. 10. Mean angular deviations for three size groups of six jack mackerel during a 54-hr period under constant illumination. Each point represents 2 hr and is an average of 12 individually calculated mean angular deviations. Time scale indicates midpoint of each 2-hr period. Mean length of fish in each group was: A, 69 mm; B, 84 mm; and C, 106 mm standard length.

that the relation between the two indices is variable (Fig. 11). Most of the variability is caused by the inclusion in separation distance of measurements of the distances between groups within a school (Fig. 11, B and C). The relationship between the two indices was more variable before than after feeding because widely spaced schools more frequently form subunits than do compact schools. Since an increase in density of a school can include both the disappearance of subunits and a decrease in distances among neighbors, separation distance can be a more powerful tool for detecting changes in compactness. Separation distance, however, is affected by both the size and the number of individuals in a school; distance to nearest neighbor, on the other hand, is unaffected by these variables. In the measurements of distance to nearest neighbor, a slight bias exists in the present data which is related to size because the distances are measured between the midline of the body rather than from the outer edge. In the present application this difference seems unimportant. For comparison of fishes that differ greatly in size, as adults and juveniles,

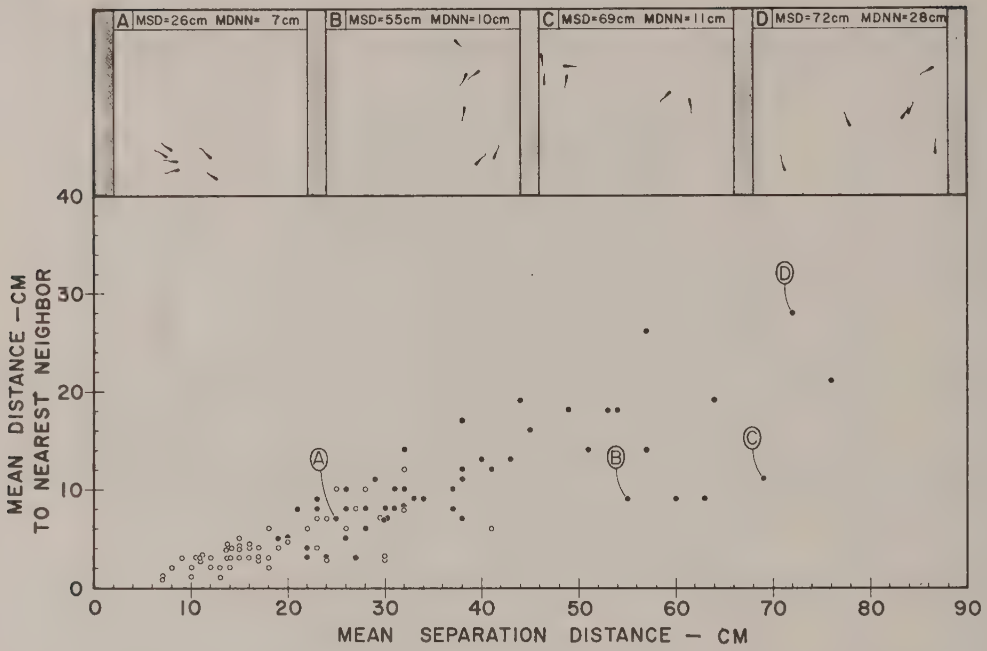


FIG. 11. Relation between mean distance to nearest neighbor (MDNN) and mean separation distance (MSD). Data were taken from the first feeding of group C: sets 1–2 (before feeding), solid circles; and sets 7–8 (after feeding) open circles. The positions of the fish in the photographs that produced points A–D are shown above figure. Points A and D are representative of those which showed a nearly constant relationship between the two indices, and B and C are divergent points.

this bias could be corrected by adjusting the measurements for average body width.

In summary, separation distance and distance to nearest neighbor have complementary functions because comparisons of them yield information on the formation of subgroups. Each has a specific function, however; for a relative measure of changes in spacing of an entire school, separation distance is preferable, but for a comparison of samples containing different numbers of individuals or individuals that differ greatly in size, distance to nearest neighbor must be used.

The parallel alignment of individuals in a school has either been excluded from measurements of schooling (Keenleyside, 1955) or it has been included in the method of measuring dispersion or spacing (Breder, 1954; John, 1964). Mean angular deviation permits an independent analysis of the alignment of individuals in a school. Unlike separation distance, mean angular deviation is independent of the size of individuals. It is, however, somewhat affected by the number of individuals in a sample. The mode of a frequency distribution of 1 million values of mean angular deviation based on six randomly determined angles per sample was 69°, but that based on 12 angles per sample was 75°.

Thus, the probability of obtaining low values of angular deviation from random data is somewhat greater if a school of 6 rather than 12 fish is used. Since this difference becomes negligible in larger schools, adjustments probably need be considered only in laboratory studies where school size is small.

For schools in which the uniformity of orientation is in doubt it may be desired to test for the randomness of the orientation. A frequency distribution of randomly determined values of angular deviation must be computed for this purpose. The number of random angles used to compute each mean angular deviation must equal the number of fish in the school. This distribution can then be compared to the data by a goodness of fit test; a significant departure of the data from the random distribution of angular deviation would indicate that the fish were oriented nonrandomly.

Data from this study showed that angular deviation was more useful than either separation distance or distance to nearest neighbor for recording behavior of schools during turns and during the initial stage of feeding, and for measuring the effect of size of individuals on schooling behavior. Angular deviation would not be useful to quantify the behavior of schools in which the fish usually do not show parallel alignment. It might help a comparative study of schooling behavior, however, because a continuum of forms exist, ranging from those that show no parallel alignment to the practically uniform schools of clupeids and scombroids (Atz, 1953).

Swimming-speed determinations (Steven, 1959) would be a useful supplement to the information provided by the three indices. Undoubtedly, both the distance among fish and orientation of the individuals in the school are influenced by swimming speed. Compared with the other indices, however, swimming speed requires much more time to calculate and also has the disadvantage that a continuous series of frames must be taken.

The methods described were designed for the analysis of the movements of fish in the horizontal plane only. There is no reason, however, that this approach could not be used to analyze vertical photographs of schools. The horizontal component was selected for this study because of the apparent importance of lateral orientation and because I plan to use this method for the analysis of films of schools taken from the air.

ACKNOWLEDGMENTS

The coordinate reader and digitizer was made available through the courtesy of the U.S. Navy Electronics Laboratory, San Diego. Warren A. Simmons of the computer section instructed in the operation of the reader. Richard R. Whitney, Tuna Resources Laboratory, provided editorial and statistical advice; C. M. Breder, Jr., Kenneth John, and Garth I. Murphy read the manuscript and offered helpful suggestions. Jack Mahan assisted in the study in numerous ways.

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LIVE COLORATION OF A JUVENILE *URASPIS SECUNDA* (POEY) FROM THE EASTERN TROPICAL PACIFIC

No record of the juvenile coloration of live *Uraspis secunda* exists (F. H. Berry, pers. commun.). A single specimen, 109 mm SL, was collected by us 10 miles southwest of Punta Guionos, Costa Rica (lat. 09° 45′N, long. 85°43′W). Upon capture, the fish was placed in a bucket of seawater and 10 minutes later color notes and color photographs were made of the live animal. Its basic body coloration was black. Posterior to the head the body coloration was broken into eight black bars by eight gold spaces (Figure 1). The gold interspaces were expanded at their dorsal and ventral ends. The third interspace extended through but not past the scaly sheath covering the base of the second dorsal fin; the dorsal ends of the interspaces 4–7 also extended through only the scaly sheath of the second dorsal fin but their ventral ends extended into the rays of the anal fin. On each of the first five black bars were two

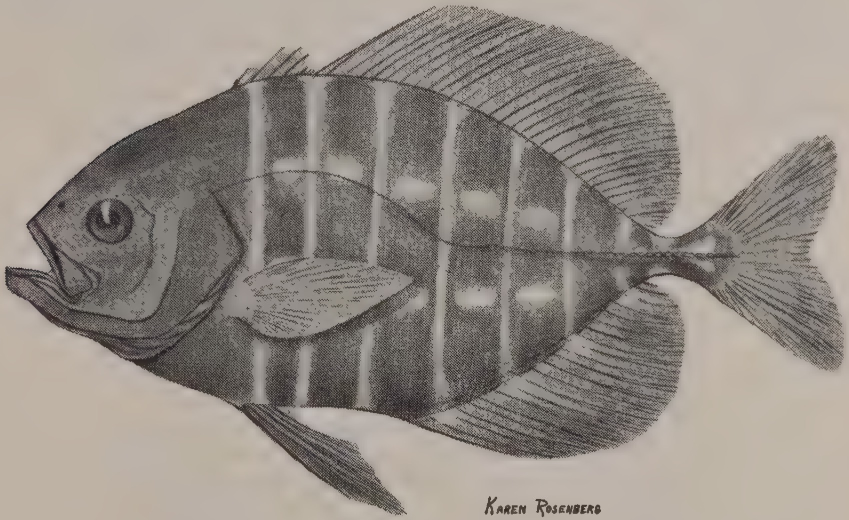

FIGURE 1.—Live coloration of a juvenile *Uraspis secunda*. All shaded areas in the figure were black in the live specimen and the white areas were gold.

oblong gold spots, one below, the other above or through the lateral line. There was a single triangular gold spot on the caudal peduncle. All fins were black; the axial margin of each pectoral fin was transparent. The inside of the mouth was white.

The fish died shortly after the photographs were taken, about 30 minutes after it was captured. After death, the body color changed rapidly from black to a sooty-yellow. The two rows of spots and the spot on the caudal peduncle became scarcely discernible, and a black nuchal band appeared that extended to the dorsal portion of the eye. Three months later, after preservation in alcohol, the nuchal band was still present but none of the spots was visible.

This fish was among other juvenile fishes captured in a miniature purse seine. The seine was set around a sheet of black vinyl that was suspended on the surface by floats, and was fastened to a mooring for 3 days during experiments on the attraction of fishes to moored objects. Juvenile *Uraspis* may show a habit like many other juvenile carangids of congregating beneath floating materials.

When out of water, *Uraspis* frequently produced sounds similar to the croaks emitted by sciaenids. The croaks were audible at a distance of 3 meters.

This is the first record of this species from inshore areas of the eastern tropical Pacific (F. H. Berry, pers. commun.). The specimen is in the Marine Vertebrates Collection of the Scripps Institution of Oceanography (S10 65-187-42A). Karen Rosenberg prepared the drawing; Frederick H. Berry read the note.

—*John R. Hunter and Charles T. Mitchell, Bureau of Commercial Fisheries Tuna Resources Laboratory, La Jolla, California.*

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Abstract

3. USE OF A SUBMARINE TO RECORD MARINE BIOLOGICAL SOUNDS

Four dives were made by the 17-ft long, two-man research submarine *Asherah* in Hawaiian waters off the leeward coast of Oahu in order to (1) evaluate the potential of using a submarine to record marine biological sounds, and (2) acoustically survey aggregations of marine animals encountered by the submarine. Acoustic data were collected at depths of 170-350 ft. Four known or suspected sound-producing fish of the families Holocentridae and Balistidae were seen at the precise locations of tape recording. The sounds recorded were similar to those previously reported for closely-related species. The four sound producers were: *Myripristis chryseres, Holocentrus lacteoguttatus, Holocentrus* sp. (*ensifer?*), and *Balistes bursa.* Spectrographic analysis of the recordings showed the presence of fixed-interval staccato sounds and variable-interval grunt-like sounds. The recordings were made by using a hydrophone mounted on struts projecting from the bow of the submarine and a portable amplifier and tape recorder located inside the 5-ft diameter pressure hull. Skillful piloting succeeded in placing the hydrophone within the small caves containing the sound-producers. The dives demonstrate the feasibility of using a submarine to carry out studies on the acoustic behavior of marine animals.

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MOLTING OF EUPHAUSIID SHRIMPS: SHIPBOARD OBSERVATIONS

by Charles W. Jerde and Reuben Lasker

Molting of Euphausiid Shrimps: Shipboard Observations[1]

Lasker (1964) showed that the planktonic crustacean *Euphausia pacifica* molted on the average every five days in the laboratory ashore. Dry molt weights were about 10% of dry weights of whole animals. He indicated that the molts might contribute substantially to the organic dertitus of the sea if this molting frequency is usual among euphausiids. We were able to obtain molting information on euphausiids not readily available to shore laboratories to compare with information from his investigation ashore. Our shipboard study extends the observations on *E. pacifica* and includes information on six other euphausiids (*E. eximia, E. recurva, E. gibboides, Thysanoessa spinifera, Nyctiphanes simplex,* and *Thysanopoda aequalis*).

METHODS AND MATERIALS

Shipboard observations were made during Cruise 6402 of the Scripps Tuna Oceanography Research program in August 1964 and Cruise 6501 of the California Cooperative Oceanic Fisheries Investigations in January 1965. A micronekton net with

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[1] This paper represents one of the results of research of the California Cooperative Oceanic Fisheries Investigations conducted under the Marine Life Research Program of the Scripps Institution of Oceanography and the California Current Resources Laboratory of the Bureau of Commercial Fisheries. We thank Warren Wilson for his assistance on shipboard, Richard A. Schwartzlose and Dr. Maurice Blackburn for ship time and facilities, and Dr. Edward Brinton for criticism of the manuscript.

TABLE 1. *Collection data for euphausiids used in this study*

Cruise No.	Date	Location		Depth (m)	Type of haul
		N lat	W long		
6402	5 Aug 1964	26°58′	115°31′	0–145	oblique
	8 Aug 1964	25°33.8′	113°45′	0–125	oblique
	13 Aug 1964	23°13.5′	112°18′	0–131	oblique
6501	6 Jan 1965	33°21.4′	118°09.1′	7	horizontal
	13 Jan 1965	34°17.8′	130°40.5′	0–140	oblique
	16 Jan 1965	33°54.0′	126°36.0′	0–140	oblique
	18 Jan 1965	35°17.8′	121°57.4′	0–91	oblique
	30 Jan 1965	31°40.5′	116°47.0′	11	horizontal

mouth opening of 2.3 m^2 and net mesh 5.5 × 2.5 mm was used for the first two of three pertinent tows on Cruise 6402. The third tow of the 1964 cruise and all tows in which euphausiids were collected on the 1965 cruise were made with a plankton net of No. 30 XXX grit gauze, with a 1-m mouth diameter. All tows were at night. Dates, geographic positions, and types of hauls are given in Table 1. After animals were brought on board, the methods of Lasker and Theilacker (1965) were used to maintain euphausiids in containers except as indicated below.

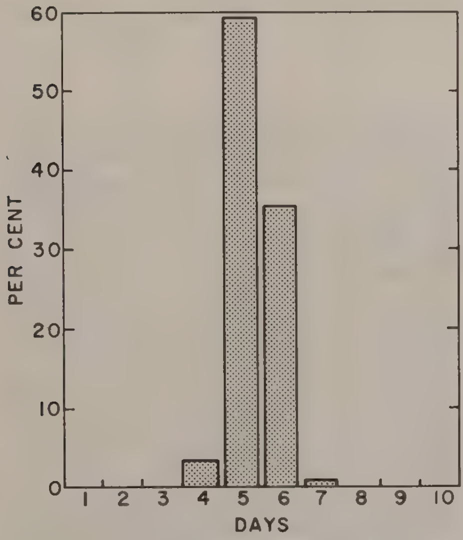

FIG. 1. Mean molting frequency of 59 euphausiids.

Only *E. eximia* were observed on the 1964 cruise. Immediately after capture, the live animals were transferred to 750-ml polyethylene containers of seawater and placed in the ship's refrigerator. The refrigerator temperature varied from 11.0 to 17.5C. At the three stations where *E. eximia* were collected, sea temperatures varied from 19.9 to 22.8C at the surface, and from 10.7 to 13.2C at 100 m. Seawater was changed daily at midnight. No food was placed in the containers to supplement that in the seawater. On both cruises the seawater, which was collected at the surface, was cooled to the temperature of the ship's refrigerator before the change of water.

On the 1965 cruise we collected and observed molting of 6 species of euphausiids. Immediately after capture, the live animals were transferred to 2,000-ml polyethylene containers and placed in the ship's refrigerator. Refrigerator temperatures varied from 8.3–12.2C. Over the geographic range of the collections, sea temperatures varied from 12.7 to 16.5C at 10 m depths and from 9.6 to 15.8C at 100 m. Seawater was changed every three days between 1300 and 1500 hr. Some animals were given no supplementary food; others were fed newly hatched nauplii of brine shrimp (*Artemia salina*).

Molts and animals were removed from seawater containers with a fine probe and washed briefly in distilled water before drying. During the 1964 cruise, molts and carcasses were placed immediately on glass slides for drying. On the 1965 cruise, they were frozen in 1-ml polyethylene containers

TABLE 2. *Molting frequency of euphausiids and weight and ash content of molts*

No.*	Species	Days alive on shipboard	Dry wt of euphausiid (mg)	No. of molts	No. of intermolt periods	Mean intermolt duration (days)	Molts			
							Dry wt all molts (mg)	Average wt (mg)	Per cent of euphausiid dry wt	Ash (%)
1	*Euphausia pacifica*	19	1.675	3	2	6	0.574	0.191	11.4	—
2		26	0.802	4	3	5	0.259	0.065	8.1	—
3		12	2.810	2	1	5	—	—	—	—
4		23	1.911	3	2	6	0.489	0.163	8.5	—
5		19	1.652	3	2	6	0.287	0.096	5.8	—
6		19	1.710	3	2	5	0.404	0.135	7.9	—
7		16	1.870	2	1	5	0.391	0.196	10.5	—
8		27	1.853	4	3	6	0.465	0.116	6.3	45.0
9		12	1.534	2	1	6	0.420	0.210	13.7	—
10		19	1.448	3	2	6	0.584	0.195	13.5	—
11		16	1.395	2	1	5	0.454	0.227	16.3	—
12		15	1.782	2	1	5	0.277	0.139	7.8	—
13		15	1.411	2	1	5	0.184	0.092	6.5	—
14		16	1.646	3	2	5	0.540	0.180	9.9	—
15		16	1.681	2	1	5	0.396	0.198	11.8	37.8
16		12	1.468	2	1	5	0.484	0.242	16.5	46.2
17		15	1.898	2	1	5	0.382	0.191	10.1	—
18		16	1.183	2	1	5	0.151	0.076	6.4	24.4
19		15	1.219	2	1	5	0.500	0.250	20.5	50.0
20		19	1.611	3	2	6	0.393	0.131	8.1	—
21		6	2.864	2	1	6	0.579	0.289	10.1	—
22		14	2.003	3	2	6	0.852	0.284	14.2	—
23		23	1.941	4	3	5	0.819	0.205	10.6	—
24		32†	2.277	5	4	6	0.913	0.183	8.0	—
25		13	2.299	2	1	5	0.491	0.246	10.7	—
26		19	2.268	4	3	5	0.892	0.223	9.8	45.7
27		44†	1.199	7	6	6	1.268	0.181	15.1	56.1
28		10	2.685	2	1	5	0.461	0.231	8.6	—
29		21	1.471	3	2	5	0.469	0.156	10.6	—

* Euphausiids 1–22, 57, 59–60—seawater changed every three days, no food added; 23–40, 51, 52, 54–56, 58, 61—seawater changed every three days, newly hatched brine shrimp nauplii added as food; 41–50, 53—seawater changed daily, no food added.

† Animals killed to terminate the experiment.

for transport to the shore laboratory, where they were placed on glass slides. Before weighing, specimens were dried to a constant weight over silica gel at 60C. To determine ash content, molts were combusted in platinum crucibles at 550C and the residue weighed.

RECORDS OF MOLTING

E. pacifica ranging in length from approximately 8 to 12 mm yielded the most information on molting frequency; data were obtained on three other species, *E. eximia*, *Nyctiphanes simplex*, and *Thysanoessa spinifera* for comparison. Individuals of three additional species, *E. recurva*, *E. gibboides*, and *Thysanopoda aequalis*, molted only once and died soon afterwards, but the weights of molts and animals are included here to show the amount of material shed during molting. *Nematoscelis tenella* and *Stylocheiron abbreviatum* caught 400 miles (720 km) offshore did not molt on shipboard and died within six days.

The molting frequencies of 55 euphausiids are presented in Table 2. Fig. 1, a composite per cent histogram of mean molting frequency, includes 40 specimens of *E. pacifica*, eight *E. eximia*, three *Thysanoessa spinifera*, three *Nyctiphanes simplex*, and four unidentified euphausiids that molted more than once.

The molting frequency of all these species was remarkably constant and appeared to be largely independent of the size and weight of the animals and the fluctuations

TABLE 2 (Continued)

No.*	Species	Days alive on shipboard	Dry wt of euphausiid (mg)	No. of molts	No. of intermolt periods	Mean intermolt duration (days)	Molts			
							Dry wt all molts (mg)	Average wt (mg)	Per cent of euphausiid dry wt	Ash (%)
30		23	1.448	3	2	5	0.717	0.239	16.5	—
31		19	1.853	4	3	5	0.633	0.158	8.5	—
32		15	1.929	2	1	5	0.457	0.229	11.8	—
33		44†	1.503	8	7	5	1.813	0.227	15.1	50.0
34		14	1.471	2	1	5	0.435	0.217	14.8	43.1
35		27	1.881	5	4	5	1.091	0.218	11.6	51.9
36		30	2.140	5	4	5	1.372	0.274	12.8	56.0
37		44†	1.798	7	6	6	0.935	0.134	7.5	—
38		20	1.151	4	3	5	0.724	0.181	15.7	54.7
39		17	2.089	3	2	5	0.648	0.216	10.3	49.1
40		16	1.433	2	1	5	0.338	0.169	11.9	54.7
41	*E. eximia*	11	19.62	2	1	6	—	1.34	6.8	—
42		19	14.03	2	1	5	—	—	—	—
43		13	17.50	2	1	6	—	1.06	6.1	—
44		11	11.93	2	1	5	—	0.72	6.0	—
45		15	12.12	2	1	5	—	0.67	5.5	—
46		13	9.090	2	1	4	—	0.70	7.7	—
47		8	—	2	1	5	—	—	—	—
48		11	—	2	1	6	—	—	—	—
49		13	—	2	1	6	—	—	—	—
50	*Thysanoessa spinifera*	20	6.070	4	3	5	2.616	0.654	10.8	43.4
51		20†	6.439	3	2	6	2.260	0.753	11.7	53.0
52		20†	5.710	4	3	6	2.877	0.719	12.6	—
53	*Nyctiphanes simplex*	14	0.854	2	1	7	0.267	0.134	15.7	—
54		20†	0.524	3	2	5	0.186	0.062	11.8	—
55		20†	0.365	3	2	5	0.121	0.040	11.0	—
56	*E. gibboides*	8	6.470	1	—	—	0.499	0.499	7.7	—
57	*E. recurva*	7	1.106	1	—	—	0.077	0.077	7.0	—
58		7	3.837	1	—	—	0.229	0.229	6.0	26.4
59		6	1.419	1	—	—	0.211	0.211	14.9	—
60		5	2.140	1	—	—	0.264	0.264	12.3	24.6
61	*Thysanopoda aequalis*	4	4.081	1	—	—	0.215	0.215	5.3	26.4

in food supply that could be maintained on shipboard. Providing *Artemia* nauplii as food seemed to prolong the lives of euphausiids but this additional food seemed to have no significant effect on molting frequency (Table 2). All of the euphausiids molted at four- to seven-day intervals but most frequently at five and six days (Fig. 1). Although no records of time of molting were made at sea, observations in the laboratory indicate that molting occurs chiefly at night. Temperature may have had an effect on the molting rate, but because animals were examined only once a day, slight changes in rate may have been missed.

The amount of material shed during the molting of 39 individual *E. pacifica* averaged 10.9% with a median of 10.6% (5th percentile = 6.3% and 95th percentile = 16.5%) of the dry weight of the animal. *E. eximia* lost an average of 6.4% of the body weight (range 5.5–7.7% for five animals) during molting; *E. recurva* (four animals) lost 10.1%; *Thysanoessa spinifera* (three animals), 11.7%; *N. simplex* (three animals), 12.8%; and losses for *E. gibboides* and *Thysanopoda aequalis* were 7.7 and 5.3%, respectively (one animal each; for detail *see* Table 2).

Ash accounted for about half of the weight of the molts in most specimens analyzed, but some ash contents as low as 25% indicated a high organic content (Table 2). Euphausiids themselves have a much lower ash content, about 10% of the dry weight.

CONTRIBUTION OF MOLTS TO DETRITUS

These data support the contention of Lasker (1964) that molting of euphausiids may contribute considerably to the mass of detritus in the sea. The molting periods of several species on shipboard were about the same as observed in the laboratory for *E. pacifica*. Brinton (1962) reported that *E. pacifica* is abundant in the North Pacific Drift and the California Current, and also occurs in the Sea of Japan, Bering Sea, and Gulf of Alaska. By contrast, *E. eximia* is endemic to the eastern equatorial Pacific Ocean and is regarded as a warm-water species. *Thysanoessa spinifera* is almost wholly neritic, occurring in coastal waters from the Aleutian Islands to Baja California. *Nyctiphanes simplex* occurs in nearshore waters of the subtropical portions of the California and Peru currents and in the Gulf of California. Thus, euphausiids living in a variety of neritic and oceanic habitats show similar regularity in molting in the laboratory environment. With the exception of *T. spinifera,* all of the species examined are known to migrate diurnally to the upper water layers, and their maximum concentrations are found at night above 140 m; *T. spinifera* appears to be restricted to the upper 100 m (Brinton 1962). Therefore, if molting occurs at night, the molts are probably released mainly in the upper layers.

Brinton (personal communication) has estimated the live biomass of *E. pacifica* alone to be about 1 g/m^2 over its broad geographical range (1.3×10^{13} m^2) during the summer. On the basis of this figure and an average determined water content of 80%, the dry weight of *E. pacifica* is 0.26×10^{13} g. At a mean molting frequency of five days, the molts would contribute about 1.9×10^{13} g/year, or almost 1.5 g m^{-2} year^{-1}.

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Chapter 33

Marine Mammals

Murray L. Johnson, Clifford H. Fiscus,
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Marine mammals are used by the Eskimos for food and clothing and as a source of income. They are the most important item among natural resources. Data were secured on nine species, but only the ringed seal and bearded seal were taken in numbers. The ringed seal is present in abundance from November through June. Pups are born in late March. Mating, with an 86.7% pregnancy rate, occurs in April and May. Food is principally fish in the winter and invertebrates in the spring, and many species of both are used. The bearded seal is present in numbers only in June. Pups are born in late April and are completely molted. Food is principally invertebrates of many species. All marine mammals are migratory, and most of the animals used by the Eskimos are absent in the ice-free months.

The study of marine mammals was made primarily in the villages of Kivalina and Point Hope. The experience of local hunters was used in our study, and large numbers of animals were examined. In August and September of 1959, Murray Johnson and Mrs. Johnson spent 3 weeks in Kivalina and 1 week in Point Hope. The Johnsons interviewed local residents and examined the seas and beaches to learn the general pattern of occurrence and utilization of marine mammals in the Cape Thompson area. In April 1960 they spent 3 weeks in Point Hope and a few days in Kivalina investigating whaling and other hunting activities.

The need for full-time resident biologists was clearly established, and Ostenson and Barbour were assigned to Point Hope for the major hunting season, November 1960 through June 1961. Johnson made one visit to Point Hope in January 1961, when aerial census surveys were instituted. Dale Rice, cetacean specialist for the U. S. Fish and Wildlife Service, spent 3 weeks with Ostenson and Barbour in April 1961.

Biological specimens and data were obtained from more than 2200 marine mammals, most of which were secured at Point Hope during the winter and spring of 1960-1961. Some specimens were secured during the preliminary studies at Point Hope and Kivalina. Two species were obtained in numbers sufficient for extensive study—the ringed seal (2028 specimens) and the bearded seal (208 specimens). Specimens and limited data were also obtained on the following: ribbon seal (7 specimens), fur seal (3 specimens), harbor seal (3 specimens), walrus (2 specimens), beluga (5 specimens), bowhead whale (3 specimens), and polar bear (3 specimens).

Working closely with the Marine Mammal Laboratory of the U. S. Fish and Wildlife Service in Seattle, we have analyzed our data to correlate field observations with final conclusions.

Historically, we find mention of marine mammals in most publications on arctic Alaska. These notations are scattered and fragmentary but are important in piecing together data on the occurrence of species. The reports of Scammon (1874), Nelson and True (1887), Bailey and Hendee (1926), Rainey (1945), and Bee and Hall (1956) have considerable general information concerning the marine mammals of northern Alaskan shores.

Authors of recent checklists of mammals who have brought together information on the general distribution and nomenclature of the marine species include Anderson (1946), Ellerman and Morrison-Scott (1951), Miller and Kellogg (1955), and Hall and Kelson (1959).

The biology and utilization of some Canadian eastern arctic species of seals have been investigated by personnel of the Fisheries Research Board of Canada, notably McLaren (1958a, b, and c and 1961). These reports are invaluable for comparative purposes.

Scheffer's (1958) review of the Pinnipedia is the best single volume regarding seals. Slijper's (1962) work contains much good general information about whales.

The Russians continue to publish results of their arctic research. Since these works involve areas closely related to our particular geographic region, they are of considerable interest. The most important of these are Naumov and Smirnov (1936), Ognev (1935), Nikulin (1940), Bobrinskii *et al.* (1944), and Tomilin (1957).

There has, however, been no previous organized study of the marine mammals of arctic Alaska. This report is the result of teamwork and is the product of many individuals.

The following list includes all species of marine mammals that have been reported from the northern Bering Sea and the Alaskan–Siberian Arctic Ocean. The habits and distribution of many of these species are poorly known; it is conceivable that individuals may at times occur in that part of the Arctic Ocean north of Bering Strait (Chukchi Sea).

The following is a list of species that may occur in the Chukchi Sea:

Species	Distribution
ORDER PINNIPEDIA	
Steller sea lion *Eumetopias jubata* (Schreber, 1776)	North Pacific, Bering Sea. Reported from Herschel I., Y. T. (McEwen, 1954—sight record.)
Northern fur seal* *Callorhinus ursinus* (Linnaeus, 1758)	North Pacific. Reported from Yukon and Northwest Territories (McEwen, 1954; Radvanyi, 1960).

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*Species known to occur in the Chukchi Sea.

Walrus* *Odobenus rosmarus* (Linnaeus, 1758)	Circumpolar, arctic.
Harbor Seal, spotted seal* *Phoca vitulina* Linnaeus, 1758	Circumpolar, arctic, and temperate.
Ringed seal* *Pusa hispida* (Schreber, 1775)	Circumpolar, arctic.
Ribbon seal* *Histriophoca fasciata* (Zimmermann, 1783)	North Pacific, primarily Asian subarctic.
Bearded seal, ugruk* *Erignathus barbatus* (Erxleben, 1777)	Circumboreal, arctic.
ORDER CETACEA	
SUBORDER ODONTOCETI	
Baird's beaked whale *Berardius bairdii* Stejneger, 1883	Pacific, north to St. Matthew Island.
Bowdoin beaked whale *Mesoplodon bowdoini* Andrews, 1908	Pacific (Bering Sea).
Goose-beaked whale *Ziphius cavirostris* G. Cuvier, 1823	Circumboreal, eastern Bering Sea.
Sperm whale *Physeter catodon* Linnaeus, 1758	Pribilof Islands, south; worldwide.
White whale, beluga* *Delphinapterus leucas* (Pallas, 1776)	Circumboreal, arctic.
Narwhal* *Monodon monoceros* Linnaeus, 1758	Arctic, mainly Canadian. (Geist, Buckley, and Manville, 1960.)
Porpoise *Stenella styx* (Gray, 1846)	Circumboreal, subarctic (Bering Sea).
Right-whale porpoise *Lissodelphis borealis* (Peale, 1848)	Eastern North Pacific (Bering Sea).
Pacific killer whale* *Orcinus rectipinna* (Cope, 1869)	Eastern North Pacific into Arctic (Scammon, 1874).
Harbor porpoise* *Phocoena vomerina* Gill, 1865	Eastern North Pacific. Point Barrow (Miller and Kellogg, 1955).
SUBORDER MYSTICETI	
Gray whale* *Eschrichtius gibbosus* Erxleben, 1777	North Pacific into Arctic (Maher, 1960).
Common finback whale* *Balaenoptera physalus* (Linnaeus, 1758)	All oceans, mainly subarctic, Chukchi Sea (Tomilin, 1957).

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*Species known to occur in the Chukchi Sea.

Sei whale* *Balaenoptera borealis* Lesson, 1828	All oceans, Chukchi Sea (Tomilin, 1957).
Little piked whale* *Balaenoptera acutorostrata* Lacepede, 1804	All oceans, Chukchi Sea (Scammon, 1874; Tomilin, 1957).
Blue whale *Sibbaldus musculus* (Linnaeus, 1758)	Circumboreal (Bering Sea).
Humpback whale* *Megaptera novaeangliae* (Bovowski, 1781)	Circumboreal, Chukchi Sea (Tomilin, 1957).
Pacific right whale *Eubalaena sieboldii* (Gray, 1864)	North Pacific (Cape Prince of Wales).
Bowhead whale* *Balaena mysticetus* Linnaeus, 1758	Circumboreal, arctic.
ORDER CARNIVORA	
Polar bear* *Thalarctos maritimus* (Phipps, 1774)	Circumboreal, polar.

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*Species known to occur in the Chukchi Sea.

METHODS OF HUNTING

Seals

Summer hunting is minimal. A few harbor seals are obtained, usually in the river estuaries or off the point at Point Hope. These may be shot from the beach or from skin boats. A few young bearded seals may be secured in the estuaries. In late October there is usually a concentration of harbor seals near the outlet of the Kukpuk River, and these are used to a degree.

Major hunting, primarily for ringed seals and occasionally for bearded seals, is done during the ice season. Great anticipation attends the forming and coming in of the sea ice. At Point Hope this is usually in early November and is synchronous with the appearance of the ringed seals, usually along the north shore. At Kivalina good ice for hunting may not be present until January. Progressive ice formation with grounding of floes along the shore means progressively good hunting. The more ice on which the hunter may travel, the more area there is for hunting. Hunting is most likely to be productive at open leads but may also be done at the seal holes. The hunter may either move along the hunting area or may wait for moving seals to pass him. Dead seals will float in the winter months and may be retrieved by hooking or by using a skin boat or kayak. In 1961 the hunters first reported seals sinking in April. By June seals sank readily and had to be retrieved by weighted grappling hooks. There is no present usage of the old methods of harpooning and netting of pinnipeds in the Cape Thompson area.

In June and early July, as the ice is breaking up, hunting is done from the large umiaks, which are powered with outboard motors. At this time the great catch of bearded seals is made, and “spring seals” (immature ringed seals) are secured in large numbers.

The rare ribbon seal and occasional walruses are secured either in the fall southward migration or, more often, in the northward migration in June. Walruses are obtained rarely during the winter.

It must be mentioned that our data regarding relative and seasonal abundance are biased because they are based on hunters’ kills. These kills, in turn, are influenced by hunter preference of species and hunting locality and, more seriously, by limitations imposed on the hunter by the rigors of his environment. Hunting is impossible many days of the season.

Whales and Polar Bears

Bowhead whales are the only large whales hunted by the Eskimos in the Cape Thompson area. Point Hope has been a traditional whaling area since prehistoric times, and hunters come from other villages to participate. At the request of several experienced whalers in Kivalina, we helped equip one team in this village in 1960. The hunt was unsuccessful although valuable data were secured through this effort.

Twenty-four-hour camps ready to spring to action when a whale is sighted are set up on the ice. When launching their umiaks and paddling up to a blind area of a whale, hunters must be absolutely quiet. Bomb lances, or “darting guns,” are thrown by hand when a boat grounds upon a whale. If the whale is “well struck,” it may die almost immediately. The hunter attempts to insert the bomb near the occipital joint or along the vertebral column. A retention harpoon is attached to a long line and a seal-skin float to signal the position of a dead or wounded whale. Whale-hunting success is limited by many factors. Inclement weather may prevent the launching of boats even when whales are visible. The open leads may close for days at a time. The whales are not easily approached, and, even when struck, they are secured only about 25% of the time. At Point Hope in 1959, only one whale was secured; in 1960 four were secured, and in 1961, two.

The method of whaling has remained virtually the same for the past hundred years. Holmes (1857) cites the method as being commonly used by the English. It was also accepted at the time by American whalers. Scammon (1874) pictures the exact equipment we observed in Point Hope. Large shoulder guns, which fire bombs like those used in the darting gun and which date back almost as far, have been used little since a fatal accident in the early 1940’s resulted from a gun explosion. Several injuries also resulted from the use of the shoulder guns.

Belugas or white whales are killed by rifle fire and then hooked and retrieved.

Although polar bears are much sought after, they are rare. They are shot whenever encountered and may be tracked over the snow.

UTILIZATION BY ESKIMOS

The marine mammals are very important to the Eskimos of the Cape Thompson area. They are used in many different ways, and nearly every part of each animal is utilized. This is uniquely Arctic in character and has allowed the survival of the Eskimo race not only in prehistoric but also in modern times.

Skins

The bearded seal skin is a heavy, durable hide. It is used to make skin boats ranging in size from small one-skin boats up to eight-skin boats (umiaks), the largest. The skins are replaced every 3 to 5 years, and only a relatively small percentage of the skins obtained each year are used for these replacements. These skins are also used to make the soles of mukluks, which are universally of this skin, and rope and lines. All these objects are made from a dehaired hide that has been prepared by soaking in water and scraping. These skins are also used as a general utility cover to protect objects.

The ringed seal skin is thinner and more pliable than the bearded seal skin. It may be fashioned into wearing apparel with the hair left on, or it may be subjected to soaking and scraping followed by bleaching by the snow and sun. The result is an almost pure white skin that can be used in fancywork or clothing. "Seal pokes" are made by skinning the ringed seal through the mouth. The orifices are tied, and the skin is inflated for floats; or the skin is inverted and used for storage of oil and oil-preserved food.

The harbor, or spotted, seal skin is used with the hair left on for various articles of clothing. It is not usually sought by hunters although several men in Point Hope make a particular effort to secure it for personal use and sale.

The ribbon seal is not common enough to be of great importance in Point Hope. A few skins, for sale at $4.00 each at the native store for several years, were never sold. Individual fresh skins, however, sold for $25.00. The ribbon seal is so rare in Kivalina that it is unknown to several of the younger hunters.

Walruses are only sporadic in occurrence. Their hides are not used in this area for umiak covers as they are in some other Eskimo villages.

Polar bear skins are prime commercial items and are too valuable for the Eskimos to keep for personal use.

Seal Oil

Seal oil is self-rendering and is prepared by cutting the blubber into long strips and putting the strips into a seal poke or an ordinary barrel. The residual fibrous remnant from which the oil departs is considered edible. The oil may be used in cooking but is mostly used as a preservative for cooked or dried seal meat, for caribou meat, for dried fish, and for berries. Items immersed in seal oil can be kept as long as 4 or 5 years if stored in a permafrost deepfreeze or as long as a year if stored at room temperature. After about a year the oil begins to turn red but is still thought to be good. A note may be inserted here that several cases of botulism (Rabeau, 1959, Dolman, 1960), some fatal, have occurred in this general area (Kotzebue to Point Hope) from eating beluga skin preserved in seal oil. An experimental study in our laboratories by Frank Fiorino revealed no evidence that seal oil is a bacteriostatic or bacteriocidal agent to common bacteria.

Another important use for seal oil is heating. The very hot flame it generates is used to advantage by most of the villagers to burn pieces of driftwood in their stoves.

Food

Bearded and ringed seals are both standard foods in the Eskimo diet. They may be cooked or dried raw for preservation in seal pokes or cooked fresh or frozen for human and canine consumption. The harbor seal is usually prepared by the natives only for their dogs; walrus meat is also used for dog food.

Beluga and bowhead whales are used primarily as food. The skin, "muktuk," is a prime delicacy of the north, and the meat and all soft parts are used for either human or canine food.

Polar bear meat is considered very good by the Eskimos.

Income from Sale*

Whole ringed seals are sold to retail stores in Point Hope and Kivalina in limited quantities or in some cases to other villages, such as Noatak and Kotzebue. The price ranges from $6.00 to $8.50 a seal.

Ringed seal skins are sold to the stores at a price ranging from $2.00 to $4.00 for a well-prepared dried skin. Skins from unborn ringed seal are commonly obtained and are usually sold to the stores for $1.00 or $2.00 or are kept for use in making clothing. Harbor seal skins may sell for $8.00 to $12.00 a skin.

Polar bear skins had a great increase in value (from $10.00 to $20.00 a foot) during the time of this study. Polar bears are the most valuable animal obtained except for the bowhead whale.

Seal blubber is at times sold for $0.15 a pound, or $5.00 a 5-gal tin, an amount that can frequently be obtained from one fat animal. The meat of one seal, after skin and blubber are removed, may be sold for $1.50.

The prices mentioned are variable and may be different in each village.

A moderate amount of native handicraft is made with materials from marine mammals. Mukluks and parkas of seal skin are exported as are model kayaks and skin boats made of ringed seal skin. Walrus ivory, which sells at the native stores in the raw state for $3.00 a pound, is used in much of the Eskimo carving. At Point Hope baskets of baleen and face masks of whale bones are manufactured.

Generally, marine mammals are used primarily for food and clothing. Commercial uses are secondary but are quite valuable to the natives.

SEAL HARVEST AND CENSUS

Harvest

The harvest of ringed and bearded seals by the Eskimos began at the time of the formation of sea ice. The first ringed seal examined was taken Nov. 17, 1960. Ice 5 to 8 in. thick had formed and piled up along the shore north of Point Hope by that date. Winter sealing built up to a peak harvest of 532 ringed seals in February (Table 1) and tapered off to 146 in April. Spring sealing reached a climax in

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*All prices are subject to great fluctuation; the stated prices refer only to the time of our field work. An Alaskan state bounty of $2.00 has been applied to all seals. There has been a phenomenal increase in the price of seal skins.

Table 1—NUMBERS OF SEALS TAKEN AT POINT HOPE NOVEMBER 1960 THROUGH JUNE 1961 BY HUNTING AREA AND MONTH*

Month	Hunting area†											
	I	II	III	IV	V	VI	VII	VIII	IX	X	Unknown	Total
November				58(3)	11	1						70(3)
December	3	11	10	60(1)	25	17		3	1	1	2	133(1)
January	14	37	39(1)	70	57(1)	26	13	26	10(1)	13	9	314(3)
February	1	11		34	329(2)	58(2)	27	29	20	3	24	536(4)
March	4		10(3)	38(1)	97(1)	68(1)	7	2(1)			6	232(7)
April	3(1)	6	2	21	86(8)	11	12(1)	6(1)		1	10(1)	158(12)
May		3	5	26	106(7)	13	17(1)	1		3	6	180(8)
June			1	18	260(84)	228(55)	2			3	268(26)	780(165)
Total	25(1)	68	67(4)	325(5)	971(103)	422(58)	78(2)	67(2)	31(1)	24	325(27)	2403(203)

*Figures in parentheses are numbers of bearded seals. Other figures are totals of ringed and bearded seals.

†Hunting areas are shown on Fig. 1.

June; 615 ringed seals and 165 bearded seals had been taken. Before June, April produced the most bearded seals although the number was still only 12. Virtually all animals taken by the villagers were weighed and measured by the biologists. However, the June totals include an estimated 241 ringed seals and 26 bearded seals that were harvested but not measured.

An interesting shift occurred in the area of the best sealing as the season advanced. In the first months of hunting, most seals were taken north of Point Hope (areas I to IV, Fig. 1), but by February most were taken at Point Hope and south toward Cape Thompson. By June very few were taken from the north side (only 19 out of 615); these few were almost all large adults.

Table 2—DISTRIBUTION BY SEX AND MATURITY OF SEALS TAKEN AT POINT HOPE NOVEMBER 1960 THROUGH JUNE 1961

Month	Ringed Seal				Bearded Seal			
	Adult		Immature		Adult		Immature	
	Male	Female	Male	Female	Male	Female	Male	Female
November	19	21	18	8			2	1
December	61	34	21	15			1	
January	177	89	24	12		1	1	1
February	179	112	129	102		1	2	1
March	59	21	78	71	1	1	1	4
April	36	10	51	41		3	4	4
May	37	13	64	53	3	1	3	1
June	28	30	163	144	30	50	26	30
Total	596	330	548	446	34	57	40	42

A combination of factors probably accounted for this seasonal shift of harvest from north to south of the village. The earlier formation of ice that could be used as a hunting platform on the north side would result in the first hunting success in that region. Also there is a southward migration of ringed seals in the fall as the ice forms. Such movement would tend to bring them close to the Point Hope peninsula as it juts out into the Chukchi Sea. Certainly in the spring there must be a definite movement of seals into the area since the harvest includes a much higher proportion of immature animals (Table 2) than the winter harvest shows.

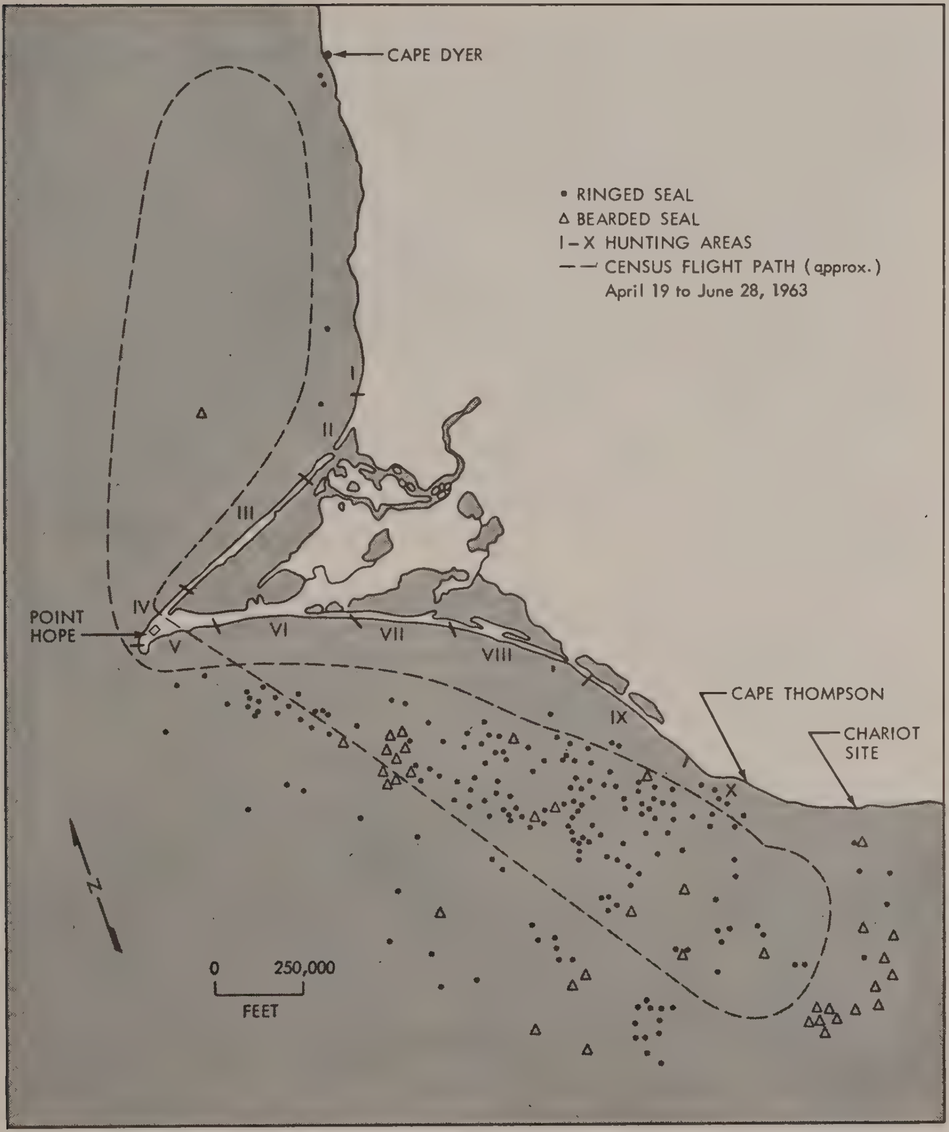
CAPE DYER
• RINGED SEAL
Δ BEARDED SEAL
I–X HUNTING AREAS
— — CENSUS FLIGHT PATH (approx.)
April 19 to June 28, 1963
II
III
IV
POINT HOPE
V
VI
VII
VIII
IX
X
CAPE THOMPSON
CHARIOT SITE
N
0 250,000
FEET

Fig. 1—Spring seal distribution and hunting area near Point Hope, Alaska.

The preponderance of males in the adult ringed seal sample is presumed to be due to greater activity and hence availability of the males to the hunters. The disparity in the sex ratio is not nearly so marked in the immature animals. By July virtually no more seals were taken. The impression given was that the ringed and bearded seals moved northwest and north and were gone from the Cape Thompson and Point Hope areas by early July.

Methods of Census

Aerial census flights were begun Jan. 18, 1961, to obtain a measure of the numbers of seals in the Cape Thompson area. Except when otherwise noted, the flights were in two loops, one north to Cape Dyer and the other south to Cape Thompson (Fig. 1). This pattern of observation was selected because it provided a basis for comparing the numbers of seals seen in different areas and because it provided observations of ice conditions north and south of Point Hope. A twin-engine plane was chartered for a 1-hr flight each week. Some weeks were missed because the plane was unavailable or the weather was unfavorable.

Normally three observers tallied seals. One rode in the copilot's seat and counted animals that dived into the water as the plane approached and animals that the plane passed over so directly that they could not be seen by the other observers, who were in the passenger compartment. From the side windows two observers each checked a strip extending a half mile out. The strip was standardized by using fixed positions at the window and by referring to fixed points on the wing of the plane. The 1-mile width of the strip covered was verified from fixed points at known distances during sweeps over land. Bearded seals were distinguished from ringed seals in the count when possible but undoubtedly were not always recognized.

The precise path followed in the various census flights was not always the same. The first few flights were exploratory, but those from February through June represented oval loops north and southeast of Point Hope. Although the general pattern of the loop flights remained fairly fixed after their initiation on February 10, the precise path followed was not always the same for all flights. Since ice conditions changed somewhat with the wind and current as well as with the advent of spring, an effort was made to select a path that represented roughly comparable ice conditions from one flight to the next. These comparable paths chosen skirted the margins of ice and open water rather than following a fixed distance from shore. The observer in the copilot's seat selected the general direction of the flight pattern and did not select spots of high seal density. The plane was flown at an airspeed of 130 to 135 knots at an altitude standardized at 300 ft. Starting on April 19, Barbour tallied the animals seen on outline maps. The approximate locations where animals were tallied are plotted on Fig. 1, which represents a sample of the sightings. By verbal communication among the observers and by records of the time of sightings, we were able to minimize duplicate counts.

Reliability of Data

Several factors doubtless affected the reliability of the data obtained. Observers may have differed as to visual capabilities even though all were experienced under arctic conditions. Differences in the altitude and speed of the plane probably caused errors in the calculated area covered. Chance variations in the availability of animals caused drastic differences in the numbers of animals sighted. For example, on March 29 at about 11:00 a. m., a pilot in a small plane flying north of Point Hope reported seeing more than 20 bearded seals and 6 ringed seals; the walrus survey crew flying a parallel route about 3 hr later tallied none. Seals on the ice were seen more clearly than those swimming in the water. Thus figures obtained when the sea was largely ice covered were not comparable with those made when much open water was present. Nevertheless, when the count is reduced to the common scale of number of seals observed per 100 square miles, reasonable consistency was usually obtained for consecutive flights (Table 3). Russian biologists report using aerial observations on seals (Tikhomirov, 1961) but give no figures or methods that can be used for comparison.

Table 3—SEALS SIGHTED ON AERIAL CENSUS ADJACENT TO POINT HOPE AND CAPE THOMPSON, 1961*

Date		Time, min	Area covered, square miles	Total number seals seen	Seals per 100 square miles†	Remarks
January	18	58	145	343	237	Entire flights between Point Hope and Cape Thompson
	25	56	140	21	15	
February	10	58	145	1	1	
	15	76	190	2	1	Flight due west about 75 miles; 1 polar bear
	22	19	47	1	2	Offshore flight from Cape Lisburne to Cape Thompson
March	1	56	140	15	11	
	8	56	140	17	12	
	22	54	135	20(1)	15	
	30	180	407	44(1)	11	Zigzag course from Cape Krusenstern to Point Hope and return
April	19	66	165	4	2	35 to 40 beluga and 3 bowhead whales seen
	28	56	140	37(2)	26	
May	8	56	140	63(12)	45	
	15	54	135	54(3)	40	
	22	50	125	75(3)	60	
	31	46	115	37(2)	32	
June	9	22	55	62(12)	113	Flight over most productive area only; flight terminated by fog
	21	60	150	43(9)	29	
	27	32	64	23	36	Offshore observations to Cape Thompson only
	28	53	133	15(2)	11	One whale (bowhead?) and one walrus
Total		1108	2711	877(47)		
Mean					32	

*Numbers in parentheses are counts of bearded seals.
†Calculated to the nearest whole number.

Numbers of Seals Counted

The general pattern of seal sightings between April 19 and June 28 is shown on Fig. 1. This figure probably is a representative pattern of late-winter and spring seal distribution but is, of course, subject to the variables noted above. Most of the locations shown were noted by Barbour and were plotted from a time log and dead-reckoning plot of each flight. The spring concentration of seals observed to the south of Point Hope is also reflected in the pattern of hunter success, as previously noted (Table 1). This preponderance of seals south of Point Hope was most noticeable after March. The scarcity of seal sightings over fast ice next to shore corresponds with information obtained on surface observations and from interviews with hunters. Seals rarely emerge on the fast ice but tend to gather adjacent to cracks and leads that occur where there is movement of the ice pack.

Bearded seals definitely recognized as such were plotted as distinct units. Concentrations of bearded seals shown off Jabbertown (area VI-VII, Fig. 1) and off the Chariot site may indicate favorable bottom-feeding conditions. That these two areas actually have concentrations of bearded seals is corroborated by the conviction among the Eskimo hunters that these are productive hunting areas for this mammal.

On 19 different flights totaling approximately 18 hr of flying time over potential seal habitat near Point Hope and Cape Thompson, 877 seals were seen on samples estimated to be 2711 square miles in total area (Table 3). This represents an average of 32 seals seen per 100 square miles of sea. Some counts varied widely from this average.

Our highest count of 237 animals per 100 square miles on January 18 apparently represented a midwinter concentration of basking seals, and, although this was our first census flight, conditions for observation may have been exceptionally favorable. The entire flight was south of Point Hope, where maximum numbers occurred throughout the season. By contrast, only a week later we had the January 25 density figure of 15 seals seen per 100 square miles, which is very close to results shown for flights in March.

The February flights were exploratory in nature and cannot strictly be compared with later flights. There is a high availability of seals during the month, as reflected in the high degree of hunter success (Table 1), but only a few were seen from the air (Table 3). On the February 10 census flight, only one seal was seen although 20 hunters brought in 51 seals on that day. During the 3 preceding days, 92 seals had been brought in. Despite this successful hunting activity, it is difficult to believe that this harvest of seals would have reduced the population so drastically that it was reflected in the aerial census figure.

The aerial census counts for March were quite uniform (11, 12, 15, 11) even though on the March 30 flight we were able to cover a more extensive area by using the equipment of the U. S. Fish and Wildlife Service walrus census crew. This flight is described in greater detail later.

Some of the spring flights showed wide fluctuations in counts. In April poor visibility and unavailability of a plane delayed our first flight until the 19th. At this time extensive leads were opening in the pack ice, and much open water was surveyed. The difficulty in identifying a swimming seal possibly was a factor in our low figure of 2 seals per 100 square miles (Table 3). The June 9 flight was terminated because of fog when only the most productive area toward Cape Thompson had been covered. This abnormally rich sample doubtless accounts for the unusually high density figure of 113 computed for this date. The remainder of the May and June flights produced counts that are roughly comparable (29 to 60) except that on June 28 the count dropped to 11. This coincided with a marked drop in the numbers of seals taken by the hunters. Virtually no ringed or bearded seals were taken by the villagers after July 1.

The walrus survey party of the U. S. Fish and Wildlife Service cooperated with us in a marine mammal survey on March 29 and 30 as an extension of our census flights. The observations discussed here and Table 4 are based on a report written by Richard H. Manville and dated May 25, 1961. The survey party included the following personnel: Karl W. Kenyon and Richard H. Manville, biologists, and Don W. Hayne, biometrician. Ostenson and Barbour accompanied them for most of the flights.

Table 4—ESTIMATES (WITH STANDARD ERRORS) BASED ON SEALS OBSERVED DURING AERIAL SURVEY* OVER CHUKCHI SEA, MAR. 29 to 30, 1961

Miles from Cape Thompson	Area, square miles	Total number of seals	Seals per 100 square miles
0-40 (entire area within 20	3,100	119 ± 53	4 ± 2
miles of shore)	1,900	119 ± 53	6 ± 3
40-80 (entire area within	9,700	354 ± 102	4 ± 1
20 miles of shore)	2,400	354 ± 102	15 ± 4
80-120 (entire area within	16,200	148 ± 90	1 ± 1
20 miles of shore)	2,700	148 ± 90	6 ± 3
Within 20 miles of path regularly flown by investigators at Point Hope	2,300	98 ± 51	4 ± 2

*Aerial survey covered about 1100 nautical miles.

The flight on March 29 started at Nome, headed across the Bering Sea past Big Diomede Island, and went across the Chukchi Sea to Point Hope. From there the flight proceeded north along the coast to Point Lay; then it moved over the Chukchi Sea west and south through Bering Strait to Nome. One walrus, six bearded seals, and five ringed seals were seen. The next day the flight began west of Shishmaref, proceeded to Cape Krusenstern and northwest by zigzag course to Point Hope, and then returned south to Kotzebue. The area from Cape Krusenstern to Point Hope and return was judged most representative of the Kivalina—Cape Thompson—Point Hope coastal area and was used as the basis of the figures in Table 3 for March 30. The census terminated over Kotzebue as the plane left the sea ice bound for Anchorage. On the second day of the census, 1 bearded seal and 62 ringed seals were tallied in the 1-mile strip covered by the observers. Estimates of populations within sectors at various distances from Cape Thompson are given in Table 4. The complete log of the two days of flying indicates that the most productive area was that adjacent to Cape Thompson between Cape Krusenstern and Point Hope although this is not shown in the sector analysis of the data of Table 4.

Summary of Flights

Our census flights indicate that almost all seals remain within a few miles of shore. The counts on different days in the same month appear to be somewhat comparable even though they are subject to wide variation. The surveys also indicate a considerable concentration of seals toward Cape Thompson in the spring of the year. When applied with caution, counts of seals by aerial census may be used as a rough index of numbers and distribution.

BIOLOGY OF THE RINGED SEAL

The biological data were derived primarily from seals secured by the hunters at Point Hope during the winter of 1960–1961. During the time that Ostenson and Barbour were resident biologists, a system was established whereby the Eskimos notified them when seals were brought in. The biologists then made rounds to each house, took desired measurements and observations, and collected specimens of skulls, teeth, claws, genitalia, stomachs, and other desired parts during the butchering. An adequate payment for this privilege produced completeness of reporting. The data therefore are derived from a total village catch for one season.

Weight

A monthly comparison of the weights of adult ringed seals (Table 5) shows a general increase in weight until midwinter and then a progressive drop through June. The adult males increased in average weight from 114.4 lb in November to 152.9 lb in January; the average weight dropped to 143.2 in February and then to 122.8 in March. They continued a gradual decline in weight, with a decided drop to 92.4 lb in June. The nonpregnant females showed a similar pattern of change but without such marked extremes. Males were heavier than the females except in June. This heavier group of females in June may have no significance since only a small sample (11) of adult females was available. Pregnant females continue their increase in size until the pups are born, and then they decrease rapidly in weight. Pregnant females in March and April averaged about 148 lb, but all nonpregnant females in April and May (including several lactating females) averaged only 108 lb. As shown by the food-habits studies, the season of maximum weight follows the period of maximum feeding activity.

Table 5— COMPARISON OF WEIGHTS* OF ADULT RINGED SEALS, NOVEMBER 1960 to JUNE 1961

	Males			Pregnant females			Nonpregnant females		
	Mean	Number	Range	Mean	Number	Range	Mean	Number	Range
November	114.4 ± 13.7	16	90–150	112.7 ± 13.7	13	95–135	92.5 ± 2.5	2	90–95
December	123.3 ± 19.0	60	75–175	123.1 ± 16.8	24	95–170	110.0 ± 14.6	8	90–135
January	152.9 ± 20.6	174	110–220	139.9 ± 18.4	79	100–190	113.9 ± 21.2	14	85–170
February	143.2 ± 26.0	187	90–210	147.6 ± 21.6	94	100–200	122.7 ± 18.0	11	95–155
March	122.8 ± 21.1	61	85–180	148.5 ± 19.1	17	110–190	108.0 ± 16.3	5	85–135
April	116.1 ± 19.3	35	90–180	147.5 ± 22.5	2	125–170	107.5 ± 12.5	6	95–130
May	114.8 ± 19.9	41	90–160				108.1 ± 25.8	13	70–165
June	92.4 ± 12.0	19	75–120				101.0 ± 16.0	11	75–130

*Means with standard deviation in pounds.

Measurements of blubber thickness (Table 6) indicate a seasonal change closely paralleling the pattern of body-weight change. This parallelism includes a later time of decrease in blubber thickness for the females in the spring (April). Blubber constitutes about half the body weight of a ringed seal in good condition. The weight of the blubber of two adults taken in March averaged 48% of the body weight. Muscle and bone constituted 37%; viscera, 10%; and the fresh skin, 5%. The blubber of an adult ringed seal taken in June was 34% of the body weight.

Table 6—COMPARISON OF BLUBBER THICKNESS* (MIDSTERNUM) IN ADULT RINGED SEALS, NOVEMBER 1960 TO JUNE 1961

	Males			Females		
Month	Mean	Number	Range	Mean	Number	Range
November	55.9 ± 6.3	20	40–72	55.3 ± 7.7	18	40–77
December	53.5 ± 8.2	63	28–72	50.3 ± 6.7	38	36–64
January	56.8 ± 8.0	174	40–74	54.4 ± 7.8	95	37–72
February	55.5 ± 8.0	183	34–75	56.6 ± 8.2	112	35–72
March	48.7 ± 6.1	55	37–62	55.2 ± 6.6	23	40–66
April	44.3 ± 6.0	39	31–56	44.9 ± 11.1	12	25–70
May	38.3 ± 6.0	38	29–58	33.4 ± 10.6	14	19–50
June	32.3 ± 5.5	33	24–50	34.1 ± 6.4	32	21–48

*Means with standard deviation in millimeters.

Length

Standard lengths of ringed seals were measured from tip of nose to tip of tail. A steel tape was stretched over the animal parallel to the long axis of the body, and the measurement was recorded in millimeters. Since lengths may vary, depending on whether the head and neck are forcibly extended or not, seals were placed in comparable positions for measuring.

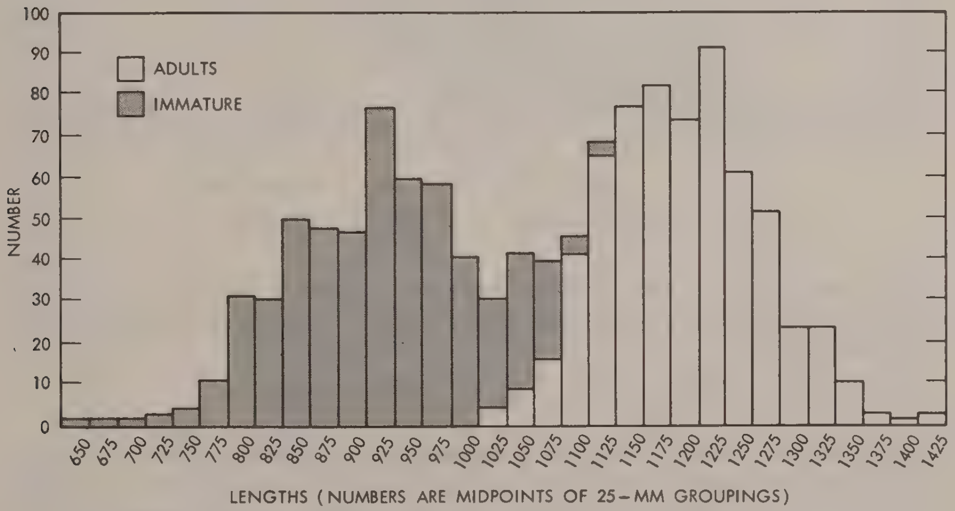

Fig. 2—Standard lengths of 1139 male ringed seals.

The lengths of 1139 male ringed seals (Fig. 2) ranged from 664 mm for a pup taken in June to 1433 mm for a large male taken in January. Lengths of 799 female ringed seals (Fig. 3) ranged from 602 mm for a pup taken in May to 1339 mm for a 15-year-old adult taken in June.

Pups measured less than 775 mm in length. Immature seals (i.e., those not yet in breeding condition) ranged to about 1100 mm. Adults were generally more than 1025 mm in length. Thus there was a zone of overlap in size between the immature and adult seals which would correspond roughly to the 5- to 7-year age groups. The twin peaks shown in the graphs depicting the size distribution (Figs. 2 and 3) indicate relatively high populations in both immature and adult populations. Relatively fewer animals were represented in the transition group.

Males were longer than females in both the immature and adult groups. The peak of the sample of immature males was reached in the 925-mm group, and that of the females, in the 900-mm group. Also, there were twice as many females (20) as males (10) in the small immature 775-mm group. This larger size of the male was a little more evident in the adults. The peak of numbers came at the 1225-mm group for males as compared with the 1175-mm group for females. Relatively few females measured more than 1250 mm, but about a fourth of the adult males were larger than this.

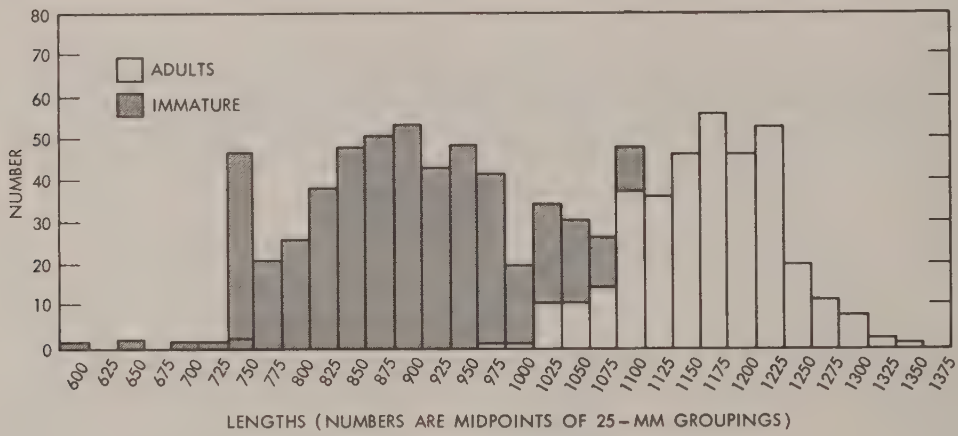

Fig. 3—Standard lengths of 799 female ringed seals.

The presence of a number of older adults in the small size groups may indicate that dwarf populations are represented as other observers (Scheffer, 1958) have noted in seals.

Food Habits

Stomachs from 1893 ringed seals collected from November 1960 to mid-June 1961 at Point Hope and 30 stomachs collected from February through March 1960 at Kivalina were examined. The results of the examinations of stomachs taken from seals at Point Hope are in Tables 7 and 8. Fishes and invertebrates found in stomachs of ringed and bearded seals are listed systematically in Tables 7 and 8. These data are combined to illustrate the differences in feeding habits between the two species. A list is included to show the taxonomic position of the food species and to give the scientific and common name when such is available.

The preserved stomach contents were washed into a sieve, and the excess fluid was allowed to drain off. The material was weighed, and the volume was measured by water displacement. The contents were then sorted by species where possible, and counts were made of each food item (actual number of larger species and estimated numbers of some of the smaller species). The percentage of total volume of each food species in the stomach was calculated for the appropriate time span (Tables 7 and 8).

Identification to species was made whenever possible, but frequently the condition of the stomach contents did not permit this degree of accuracy. The frequency of occurrence and trace occurrence, the number of times dominant (50% or more), and the largest number of the particular food species counted in any one stomach were recorded and are on file at the University of Puget Sound.

Table 7—PERCENTAGE OF TOTAL VOLUME OF FISHES FOUND IN STOMACHS OF RINGED SEALS (RS) AND BEARDED SEALS (BS), POINT HOPE, 1960–1961

	Month															
	November		December		January		February		March		April		May		June	
Species	RS	BS	RS	BS	RS	BS	RS	BS	RS	BS	RS	BS	RS	BS	RS	BS
Herring					*		*									
Salvelinus sp.															0.5	
Capelin					*						0.1					
Smelt											0.2					
Arctic cod	26.1	*	56.4		99.0	2.0	90.2	24.1	21.7		9.1		3.6		8.4	
Saffron cod	13.9		13.9		0.4		0.1		5.4		19.2		1.9		17.7	
Stickleback	0.2		*								0.3		*		0.1	
Sculpins, unspecified	2.8		*						0.3	*	2.9	*	0.8		0.2	*
Sculpin, *Artediellus* sp.			0.2				*				0.1					
Sculpin, *Gymnocanthus* sp.	0.4		1.9		0.1		0.1		0.8	1.9	1.0		1.2		*	
Sculpin, *Myoxocephalus* sp.	37.9		3.8				0.3		2.4	0.5	4.7	2.9	3.8	0.5	3.5	1.9
Fourhorn sculpin			10.7										0.1			*
Shorthorn sculpin			0.9													
Sculpin, *Triglops* sp.											0.1					
Sandlance	4.9		1.2		*		1.6	2.2	6.1	7.8	1.8		1.2		3.7	
Pricklebacks			0.1				*	0.2	0.1		0.1		0.5	0.5		
Righteye flounders									*							*
Yellowfin sole											0.1					
Starry flounder									0.6							
Unidentified material	3.5		1.3		0.3		0.7	4.8	4.5	3.2	4.2	12.0	1.6	2.4	3.3	6.5
Invertebrates†	10.3	100.0	9.6		0.2	98.0	7.0	68.7	58.1	86.6	56.0	85.1	83.9	96.6	62.5	91.6
Stomachs with food‡	30	1	99	0	248	2	439	4	168	6	119	9	100	4	229	87
Stomachs empty‡	33	2	23	0	57	0	76	0	47	0	16	3	67	4	142	42

*Trace

†Percent of total stomach contents that were invertebrates (from Table 8).

‡Also included in Table 8.

Throughout the collection area the ringed seal can probably reach the bottom. Depths of less than 10 fathoms can be found up to 2½ miles offshore in the Point Hope locality. In the vicinity of Cape Thompson, these depths extend out about 5 miles. Depths of 30 fathoms or more are found approximately 10 miles offshore in the Point Hope area. In the vicinity of Kivalina, depths of 20 fathoms or less are found up to 10 miles offshore. Open leads in the ice are irregularly present during the entire ice season; thus the seal may have a larger feeding range here than is possible in other parts of the Arctic. The shallow water in conjunction with large open leads allows the seals to select from a wide variety of benthic, nektonic, and demersal food species.

The ringed seal apparently takes whatever food species are available. Few fish over 200 mm in length were found in the stomachs; the largest invertebrates present were shrimp *(Sclerocrangon boreas)* and crabs *(Hyas* sp.*)*. These findings may indicate a preference for the smaller species, but they are also the result of the greater abundance and availability of small fish. Ringed seals did not feed to any great degree on sedentary bottom dwellers as did bearded seals.

Table 8— PERCENTAGE OF TOTAL VOLUME OF INVERTEBRATES FOUND IN STOMACHS OF RINGED SEALS (RS) AND BEARDED SEALS (BS), POINT HOPE, 1960–1961

	Month															
	November		December		January		February		March		April		May		June	
Species*	RS	BS	RS	BS	RS	BS	RS	BS	RS	BS	RS	BS	RS	BS	RS	BS
Sponges							†			1.1				†	3.0	6.4
Hydrozoa												†		†		†
Anthozoa									0.1							
Sipunculida												0.5				
Priapulida												0.5				
Echiuroidea	2.0	4.8	0.4		0.1		0.1		0.9	†	0.5	†	4.5		0.4	0.7
Annelida							†						†		0.1	0.3
Crustacea, unspecified			0.3				0.3		1.3	1.3	1.1	1.6	1.4	18.3	4.7	1.6
Mysids	0.1		0.1		†		0.3		1.9	†	4.5		27.1	†	11.7	†
Cumacea							†								†	
Isopoda			0.7				†									1.1
Amphipoda	1.3		6.2		†		0.2		24.7	0.8	25.6	2.4	15.4		6.8	†
Euphausiacea	0.1						0.1		0.8		1.2		6.1		1.6	†
Decapoda, unspecified		20.0				8.3		5.3				8.2		22.6	1.6	2.7
Shrimp	6.8	60.0			0.1	85.2	6.0	51.8	27.4	24.5	23.0	51.7	29.4	26.8	28.2	12.6
Crabs, unspecified							†									0.6
Crabs, Brachyura		5.2				†	†	1.8	1.0	2.0		13.9		24.3	3.7	24.3
Crabs, Anomura		4.8				4.5	†	2.4	†	56.3	0.2	3.8	†		0.5	1.[illegible]
Sea spider													†			
Gastropoda								6.1				†		2.3	0.2	1.6
Tectibranchiata		5.2						1.3		0.6		1.8		2.3		0.2
Octopoda									†		†			†	†	
Clams												0.7			†	27.7
Echinodermata							†									
Tunicata					†									†	0.1	†
Milk													1.4			
Unidentified material‡	3.5		1.3		0.3		0.7	4.8	4.5	3.2	4.2	12.0	1.6	2.4	3.3	6.5
Fish§	86.2		89.1		99.5	2.0	92.3	26.5	38.6	10.2	39.7	2.9	13.1	1.0	34.1	1.9
Stomachs with food‡	30	1	99	0	248	2	439	4	168	6	119	9	100	4	229	87
Stomachs empty‡	33	2	23	0	57	0	76	0	47	0	16	3	67	4	142	42

*Common names are used when available.

†Trace.

‡Also included in Table 7.

§Percent of total stomach contents that were fish (from Table 7).

There appeared to be no significant differences in feeding habits between sexes. Feeding habits by year, class, or age group were not analyzed, nor was any attempt made to break down the food-habit studies to localities. Generally speaking, the food species found in stomachs of ringed seals from the Point Hope and Kivalina areas were similar. Both areas are much alike in regard to depth of water, but no information was available on water temperature, salinity, or currents.

Pebbles varying in size from 4 to 15 mm were found in stomachs of the ringed seal during all months of the study. Some of these undoubtedly were present in the stomachs of captured prey since most gadid stomachs contained some pebbles. Some might have been obtained accidentally in the pursuit of prey.

The contents of individual stomachs varied considerably. During December, January, and February, the arctic cod *(Boreogadus saida)* was frequently the only food species present. As many as 51 nearly complete cod were found in one stomach. Fragmentary and trace remains of 125 cod were found in another stomach. In the spring the gammarid amphipod *(Ampelisca* sp.) was frequently the only food species present, and as many as 1000 occurred in a single stomach. Commonly four to five species of shrimp occurred in one stomach. As an example of the variety of food, a well-filled stomach (310 cm^3) collected Apr. 21, 1961, contained: 7 small sand lance, 4 small sculpins (*Gymnocanthus* sp. and *Myoxocephalus* sp.), 1 saffron cod, 2 pricklebacks, 2 small (34 and 35 mm) yellowfin sole, 1 unidentified fish, 200 mysids, 100 amphipods, and 22 shrimp *(Pandalus* sp., *Pandalus goniurus, Argis* sp., and *Crangon dalli).*

Stomachs from seals taken in late spring often contained only one or two small fish (30 to 40 mm), a few mysids, or occasionally one or two shrimp. A single specimen of the shrimp *(Sclerocrangon boreas)* was sometimes the only food found in a stomach. These examples and the stomachs containing a large variety of food species are indicative of random feeding.

In stomachs containing food the average monthly volume was found to be:

Month	Volume of food, cm^3	Month	Volume of food, cm^3
November	75	March	96
December	116	April	88
January	264	May	72
February	149	June	35

The highest average volumes were obtained during the 3 months when cod was the predominant food species. The abrupt drop in volume in June may have been due in part to the inclusion of stomachs from young seals, which often contain relatively little food. Other factors involved in the decrease in volume are probably the approach of the molting (fasting) season and the migration northward.

The quantity and variety of the numerous food species changed during the months of the sampling, probably because of availability of food species although food preference could be a factor.

The major species in order of monthly importance were:

Month	Species	Remarks
November	Sculpins Arctic cod Saffron cod Shrimp	Approximately 90% of the volume of the stomach contents was fish
December	Arctic cod Sculpins Saffron cod Amphipods	More than 90% of the volume of the stomach contents was fish
January	Arctic cod	Represented 99% of the stomach contents

February	Arctic cod Shrimp	Arctic cod made up 90% of the volume of the stomach contents
March	Shrimp Amphipods Arctic cod Sand lance	Nearly 60% of the volume of the stomach contents was invertebrates
April (at Point Hope)	Shrimp Amphipods Saffron cod Arctic cod	Invertebrates made up 56% of the stomach contents
(at Kivalina)	Shrimp Crabs (Brachyura) Unidentified crustacea Sculpins	Invertebrates made up 87.2% of the stomach contents
May	Shrimp Mysids Amphipods Sculpins	Invertebrates made up 84% of the stomach contents
June	Shrimp Saffron cod Mysids Arctic cod	More than 62% of the volume of stomach contents was invertebrates; 56 different food species were identified from stomachs during this month

Fish formed a major part of the stomach contents from November through February, whereas invertebrates were dominant from March through June.

Seven food items were present during the entire collection period: Arctic cod was of major importance for November, December, January, February, and March. Saffron cod replaced the arctic cod in importance during April, May, and June. Although sand lance occurred in minor quantities at all times, it became an important food species in March. Echiuroids were of minor importance during most months but in May formed 4.5% of the total stomach volume. Most echiuroid remains were in such poor condition that specific identification was impossible; however, one echiuroid from the June collection was probably *Echiurus echiurus*. Mysids were of major importance in May and June. Mysids from two stomachs collected in June were tentatively identified as *Neomysis rayi*. Gammarid amphipods were of importance during the months of March, April, and May. One identified as *Ampelisca* sp. was a major food species in March and April. Shrimp (Carides) were of major importance in the collection from March through June. Eleven species from three families were identified. Members of the family Crangonidae were important food species in March, May, and June, and members of the family Pandalidae were important food species in April. Members of the family Hippolytidae were never found in important quantities.

A classification of fishes and invertebrates found in ringed and bearded seal stomachs is given here.

Classification of Fishes Found in Ringed and Bearded Seal Stomachs

Family Clupeidae—herring
  Clupea harengus pallasi—Pacific herring
Family Salmonidae—trout, whitefish, grayling
  Salvelinus sp.—trout, char

- Family Osmeridae—smelt
  - *Mallotus villosus*—capelin
  - *Osmerus dentex* — arctic smelt
- Family Gadidae
  - *Boreogadus saida*—arctic cod
  - *Eleginus gracilis*—saffron cod
- Family Gasterosteidae
  - *Pungitius pungitius*—ninespine stickleback
- Family Cottidae—sculpins
  - *Artediellus* sp.
  - *Gymnocanthus* sp.
  - *Myoxocephalus* sp.
  - *Myoxocephalus quadricornis* —fourhorn sculpin
  - *Myoxocephalus scorpius* —shorthorn sculpin
  - *Triglops* sp.
- Family Ammodytidae
  - *Ammodytes hexapterus*—Pacific sand lance
- Family Stichaeidae—prickleback
  - *Stichaeus punctatus*— Arctic shanny (identification uncertain)
- Family Pleuronectidae—righteye flounder
  - *Limanda aspera*—yellowfin sole
  - *Platichthys stellatus*—starry flounder

Classification of Invertebrates Found in Ringed and Bearded Seal Stomachs

- Porifera (Sponges)
- Cnidaria
  - Class: Hydrozoa
    - Order: Hydroida
      - Suborder: Gymnoblastea
        - Genus: *Hydractinia**
  - Class: Anthozoa
    - Subclass: Alcyonaria
- Sipunculida
- Priapulida
- Echiuroidea
  - Genus: *Echiurus*
    - Species: *echiurus**
- Annelida
  - Class: Polychaeta (worms)
  - Hirudinea (leeches)
- Arthropoda
  - Subphylum: Mandibulata
    - Class: Crustacea
      - Order: Copepoda
      - Subclass: Cirripedia (barnacles)
        - Order: Thoracica
          - Genus: *Balanus*
      - Subclass: Malacostraca
        - Order: Mysidacea
          - Genus: *Neomysis*
            - Species: *rayi*
        - Order: Cumacea
        - Order: Isopoda
          - Genus: *Mesidotea*
        - Order: Amphipoda
          - Suborder: Gammaridea
            - Family: Gammaridae
              - Genus: *Ampelisca*

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*Identification probable.

- Order: Euphausiacea
  - Genus: *Euphausia*
    - Species: *pacifica**
  - ?*Thysanoessa*
    - Species: *longipes**
  - ?*Thysanopoda*
- Order: Decapoda
  - Suborder: Natantia (Macrura)
    - Tribe: Carides (shrimp)
      - Family: Hippolytidae
        - Genus: *Lebbeus*
          - Species: *groenlandicus*
          - *polaris**
        - *Heptacarpus*
          - Species: *tridens**
        - *Eualus*
          - Species: *fabricii**
          - *macrophthalmus**
          - *gaimardii belcheri**
        - *Spirontocaris*
          - Species: *kincaidii*
      - Family: Crangonidae
        - Genus: *Crangon*
          - Species: *dalli*
          - *septemspinosa**
        - *Argis*
          - Species: *crassa**
          - *dentata**
          - *lar**
          - *levior**
      - Family: Crangonidae
        - Genus: *Sclerocrangon*
          - Species: *boreas*
      - Family: Pandalidae
        - Genus: *Pandalus*
          - Species: *borealis*
          - *goniuras*
        - *Pandalopsis*
          - Species: *aleutica*
  - Suborder: Reptantia (crabs)
    - Tribe: Brachyura
      - Family: Maiidae
        - Genus: *Chionoecetes*
          - Species: *bairdi*, *opilio* } (tanner crabs)
        - *Hyas*
          - Species: *coarctatus alutaceus*
          - *lyratus*
      - Family: Atelecyclidae
        - Genus: *Telmessus*
          - Species: *cheirogonus* (hairy crab)
        - *Erimacrus*
          - Species: *isenbeckii* (hairy crab)
    - Tribe: Anomura
      - Family: Lithodidae
        - Genus: *Hapalogaster*
        - *Placetron**

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*Identification probable.

- Family: Paguridae
  - Genus: *Pagurus*
    - Species: *capillatus** (hermit crabs)
      brandti
      splendescens
- Subphylum: Pycnogonida (sea spider)
- Mollusca
  - Class: Amphineura (chiton)
  - Class: Gastropoda
    - Subclass: Prosobranchia (snails)
      - Family: Buccinidae
        - Genus: *Buccinum*
        - *Fusitriton*
          - Species: *oregonensis*
      - Family: Naticidae
        - Genus: *Natica*
          - Species: *clausa**
        - *Polinices*
      - Family: Lamellariidae
        - Genus: *Velutina*
          - Species: *velutina**
      - Family: Muricidae
        - Genus: *Boreotrophon**
      - Family: Turridae
        - Genus: *Oenopota**
    - Subclass: Euthyneura
      - Order: Opistobranchia
        - Suborder: Tectibranchiata
        - Suborder: Nudibranchiata (sea slug)
  - Class: Cephalopoda
    - Order: Dibranchia
      - Suborder: Octopoda
  - Class: Pelecypoda (clams)
    - Order: Teleodesmacea
      - Suborder: Diogenodonta
        - Family: Astartidae
          - Genus: *Astarte*
      - Suborder: Asthenodonta
        - Family: Hiatellidae
          - Genus: *Hiatella**
- Echinodermata
  - Class: Holothuroidea* (sea cucumbers)
- Tunicata
  - Genus: *?Boltenia*

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*Identification probable.

Reproduction

MALES The materials and methods described on the pages that follow were used in the study of reproduction in male ringed seals. The size and weight of the testes in the fresh state were determined although in small testes only the weight was recorded. The testes were then preserved in formalin. Approximately 650 microscopic sections have been prepared, mostly of adult specimens, although a generous number of samples from immature specimens have also been included. Each section contains a portion of the epididymis. The sections were examined for evidence of spermatogenesis and for sperm in the epididymis. The baculum *(os penis)* was obtained from each specimen, and the flesh was removed by boiling. Weights and lengths have been determined on 1056 specimens (Fig. 4). These data have been plotted against the time of year and age. Several samples of animals were aged by dental annuli.

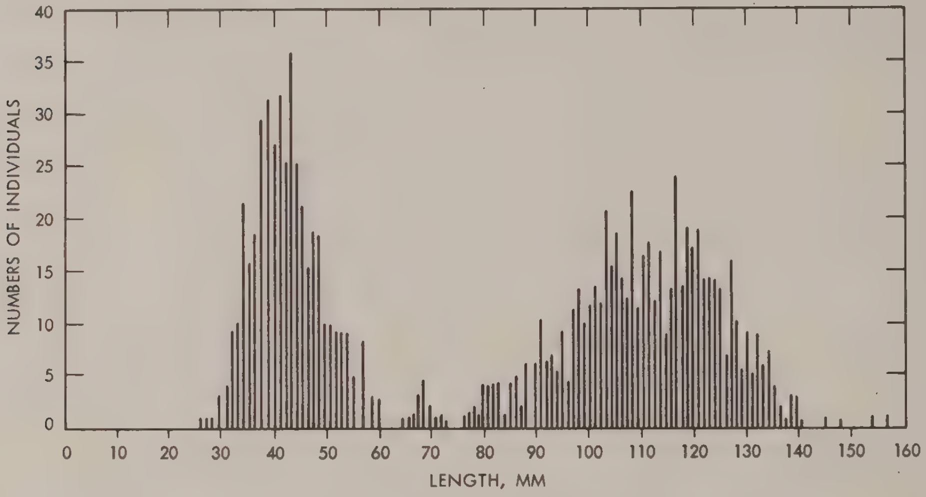

Fig. 4—Length distribution in 1056 bacula of Pusa hispida *(ringed seals).*

With these data we have attempted to understand the sexual development and activity of the male ringed seals during the months of their presence in the Cape Thompson area. We believe that completing the sampling and subjecting our data to further analysis will tend to verify the conclusions stated below. The works of McLaren (1958) have been used by us with appreciation.

Microscopic examination of the testis was considered the most accurate method of determining sexual activity. The appearance of the immature specimen, including the epididymis, was characteristic. The small 2- to 4-g testis was universally found in the 2-, 3-, and 4-year groups (Table 9). A slight increase in size was seen in the fifth year, and a moderate increase (to 9 g, average 5.9 g) was seen in the sixth year. A spurt of growth was noted in the seventh year; the testis averaged 16.2 g, the size ranging from the immature 3 g to a fully mature 37 g. Spermatogenesis was well correlated with this increase in size; none was seen in testes below 20 g. Residual sperm in the epididymis were seen, however, in one 14-g testis taken June 12. The testis itself showed an extreme degree of degeneration with no suggestion of spermatogenesis.

The testes in our samples were all immature through the sixth year. Abruptly in the seventh year most of those examined beyond March showed spermatogenesis and much sperm in the epididymis. Beyond the eighth year sperm was found in an increasing number of specimens in the epididymis during the months of December and January, the most active spermatogenesis occurring during January, February, March, April, and May. The most potent males, as indicated by the epididymides packed with sperm, were found in March, April, and early May. An increase in testis size was apparent during the active breeding months. The weight in grams may be converted into measurements in millimeters (including the epididymis) by the following representative figures: 4 g is 30 by 15 mm; 14 g is 40 by 22 mm; 20 g is 50 by 25 mm; and 40 g is 58 by 36 mm. Most of the testes of breeding animals were approximately 25 to 45 g although one unusual specimen weighed 71 g.

Table 9—RELATION OF THE WEIGHT OF TESTES (INCLUDING EPIDIDYMIDES) TO WEIGHT AND LENGTH OF BACULA IN VARIOUS AGE GROUPS OF RINGED SEAL

Age Group	Number of Specimens	Testis weights, g		Baculum weights, g		Baculum lengths, mm	
		Range	Mean	Range	Mean	Range	Mean
2 year	30	1.9–4.0	2.6	0.10–0.22	0.15	31–44	34.2
3 year	17	2.0–4.0	2.9	0.19–0.58	0.32	38–52	40.7
4 year	11	2.0–4.0	2.9	0.15–0.78	0.26	34–57	42.3
5 year	12	3.0–5.0	3.9	0.33–0.74	0.55	41–62	45.6
6 year	8	5.0–9.0	5.9	0.46–3.81	1.56	48–90	62.0
7 year	16	3.0–37	16.2	0.96–5.62	3.13	51–96	75.2
8 year	16	6.0–46	23.6	1.68–9.26	5.44	63–107	89.1
9 year	21	13.0–43	23.4	3.38–13.63	7.33	80–120	99.1
10 to 11 year	91	13.0–62	30.6	3.25–14.24	7.38	87–127	102.6
12 to 15 year	142	10.0–66	32.3	4.03–20.20	9.02	80–140	107.6
16 to 19 year	83	16.0–50	30.5	6.83–19.65	12.02	98–135	115.9
Over 20 year	48	14.0–71	33.7	6.47–21.20	13.30	101–152	124.0

The baculum is a good indicator of relative age (Table 9). According to our data there is a continuous growth of the bone throughout life, which is reflected by the weight and length. The largest percentage of growth is between the fifth and eighth years. Evidence of further growing, however, was made clear by the more than doubling in weight between the 8- and the 16- to 19-year group and an increase by a third of the average length after the 8-year group.

Figure 4 illustrates the relative age makeup of the entire population of 1056 males. The large numbers of immature and adult seals were widely separated by relatively few in the transitional size, which indicates a rapid period of growth of the baculum as maturity is achieved. The factors of availability and selectivity of hunter success must be considered in interpreting these data, but we do not believe them to be of great consequence here.

Three conclusions may be drawn regarding the sexual activity of the male ringed seal. Maturity is obtained in the seventh year. There appears to be some breeding potential in the older age groups in each of the winter and spring months, but the prime season is March, April, and May, which corresponds to the parturition dates of late March and early April. There is a striking loss of breeding potential after the first part of June.

FEMALES Maturing of the female seal was indicated by signs of ovulation. The most striking and easily recognized evidence of ovulation was the formation of the corpus luteum. If pregnancy did not occur, the corpus luteum was small and disappeared gradually. During pregnancy the corpus luteum persisted until delivery. Corpora lutea undergo cellular degeneration into corpora albicantia, which may be identifiable in the ringed seal for several years. Determinations were made by macroscopic examination of serially sliced ovaries; microscopic examination confirmed the gross appearance when necessary.

In the ringed seal the pregnancy was usually in the uterine horn on the side of the corpus luteum. It is quite well established that delayed implantation occurs, but we did not examine our specimens for blastocysts.

Table 10—PERCENTAGE OF PREGNANCY IN ADULT FEMALE RINGED SEALS COLLECTED BETWEEN NOV. 17, 1960 AND APR. 8, 1961

Month	Number pregnant	Number of adults	Percentage pregnant
November	19	17	89.5
December	34	27	79.4
January	92	79	85.9
February	111	98	88.3
March	21	17	81.0
April (to April 8)	3	2	66.7
Total	280	240	85.7

Table 11—DEVELOPMENT OF CORPORA LUTEA IN PREGNANT RINGED SEAL, NOV. 25 TO APR. 8, 1961

	Length × width		Mean
Month	Range, mm	Mean, mm	(length + width)
November	(9–16 × 5–9)	12.1 × 6.9	19
December	(11–17 × 7–15)	13.8 × 9.9	23.7
January	(8–19 × 6–16)	14.3 × 10.6	24.9
February	(11–20 × 8–16)	15.3 × 10.7	26
March	(12–16 × 10–13)	14.8 × 11.5	26.3
April	(16–19 × 7–14)	17.5 × 10.5	28

A high percentage of adult ringed seals were found pregnant (Table 10). Approximately 14% of the mature females, however, either had not conceived (missed pregnancy) or had aborted. In several cases where an abortion was fairly definite, there appeared to be a rapid regression of the corpus luteum into a large corpus albicans.

Table 11 shows the development of corpora lutea in pregnant seals between November 25 and April 8. Length increased from 12.1 mm in November to 17.5 mm in April, which is an average increase of 0.9 mm per month. The mean width increased from 6.9 mm in November to 10.5 mm in April, which is an average increase of 0.6 mm per month. If the sum of the length and width is taken for each month, an average increase of 1.5 mm per month in each corpus luteum is seen.

Follicle activity appeared to increase gradually from November. At this time the largest follicles in the ovary with the corpus luteum were 4.1 mm and in the opposite ovary were 5.4 mm. In April the follicles in the ovaries with corpora lutea measured 7 mm and in the ovaries without, 9 mm. An average increase of 0.5 mm per month occurred. In nearly all cases the ovary lacking the corpus luteum had the larger follicles.

SUMMARY OF REPRODUCTIVE STATUS BY AGE GROUP Ovaries were examined for: (1) follicular development, (2) corpora lutea size and condition (whether proliferating, mature, or regressing), and (3) corpora albicantia size and type (line, stellate, oval, or amorphous).

The ovaries from seals ranging in age from 4 to 10 years were particularly examined to determine the age at which sexual maturity occurred. Adult animals are those that have ovulated and have a corpus luteum or corpus albicans. No differentiation of adolescents was made in this study.

Fourth Year. In the 4-year group, each of the 14 specimens was immature. Only two (14%) showed any increased follicular activity. No follicles measured more than 1 mm in diameter.

Fifth Year. The 5-year group was composed of 12 animals. Eleven (92%) were classified as immature. One individual killed on January 11 had ovulated and was supporting a 9- by 9-mm corpus luteum in her left ovary. Both ovaries contained developing follicles. The right ovary had five follicles in the 3- to 4-mm range; the left had seven. The largest follicles were in the left ovary and measured 4 mm in diameter. Another on June 2 was supporting a large follicle (13 by 7 mm) in its left ovary. It is not known whether this follicle was involuting. If not, then a late ovulation would probably miss fertilization.

Sixth Year. Ten seals made up the 6-year group. Six (60%) were classified as adults. They had ovulated and were supporting corpora lutea. Specimen M1610, killed May 28, supported a large (12 by 8 mm), compact, and presumably active corpus luteum in its left ovary. The right ovary contained a corpus albicans measuring 6 by 3.5 mm. This indicates a previous ovulation in the fifth year. It is possible that at the time of death the seal was carrying an unimplanted blastocyst (as indicated by the functioning corpus luteum). Specimen M1770, killed June 3, had in its right ovary a newly formed corpus luteum 8.5 by 7 mm. Blood was still present in the antrum of the former follicle; this suggests that the ovulation had been very recent. The left ovary contained a 4-mm corpus albicans, which indicates, as in M1610, that ovulation had first occurred during the fifth year. The four remaining adults had all apparently ovulated only one time. They were killed December 20, January 15, May 21, and June 6. The December and January specimens held regressing corpora lutea 6.5 by 5 mm and 8 by 6 mm. The May specimen had a corpus hemorrhagicum in its right ovary 8 by 7 mm in diameter, and the June individual supported a recent but a regressing corpus luteum measuring 9 by 5 mm. This indicates ovulations for the first time in the sixth year. The five juveniles all showed mild follicular development.

Seventh Year. Nine animals made up the 7-year group. Five (55%) were adults. Pregnancies first occurred in this age group; three of the five adults were carrying fetuses. Of the three pregnant seals, two were killed in late January; the third was killed early in February. All fetuses were developing normally. The corpora lutea of pregnancy measured 15 by 11 mm, 13 by 10 mm, and 14.5 by 10 mm, and all appeared to be functioning normally. Two of the three pregnant adults carried one corpus albicans each. All showed high follicular activity in both ovaries, the largest follicles ranging from 3.5 to 9 mm. The two nonpregnant adults apparently had ovulated only once. Specimen M196, killed on December 22, carried a corpus albicans in the right ovary and a large 7.5-mm follicle in the left. Specimen M1322, killed on April 1, carried a regressing 7- by 6.2-mm corpus luteum; this suggests a very late ovulation in the breeding season of the past year. There were no corpora albicantia visible in either of these last two seals. The four juveniles showed mild follicular development, but no follicles measured more than 4 mm.

Eigth Year. Fourteen seals made up the 8-year series. Of these, 13 (93%) were classified as adults. The juvenile had mild follicular activity but nothing else. It was killed January 17. There were seven adult seals representing the time between December 29 and April 8. Only three of the seven contained fetuses. Of the four remaining, only one had a corpus luteum. It was killed February 21, and the corpus luteum (7 by 5 mm) was regressing. The three without corpora lutea all contained fairly large corpora albicantia (5 by 3, 3 by 3, and 3 by 3 mm), which suggests ovulations in the past season but failure of fertilization. An average of two corpora albicantia per seal was found in the three pregnant seals. Corpora albicantia occurred in five of the six ovaries. In the nonpregnant seals only 0.75 corpus albicans per seal was recorded. The three pregnant adults had corpora lutea of comparable sizes (14 by 8, 12 by 10, and 13 by 9 mm). Folliculation was active in all three, the largest follicles ranging in size from 5 to 8.5 mm. Follicular activity in the nonpregnant seals was less, the largest ranging from 1 to 6 mm in diameter. Six adults were taken between April 8 and June 28. All but one had corpora lutea. That one had a corpus albicans (5.5 by 4.5 mm) in the right ovary. The left ovary was lost. Examination of the corpora lutea suggested that not all were pregnant. Specimen M1459, killed on April 29, had a degenerate corpus luteum in its left ovary (the corpus had almost reached the albicans stage). Ovulation was suggested by the presence of a large follicle in the right ovary. The remaining four seals had recent and active corpora lutea with an average size of 9.5 by 7.2 mm. This would indicate probable pregnancies; securing the blastocysts would be the only means of confirmation. Corpora albicantia occurred in four of the six seals examined; the two without contained questionable scar tissue.

Ninth Year. There were 20 specimens in the 9-year group. All were adults, and eleven were pregnant. There was an average of 1.8 corpora albicantia per seal in this pregnant group. The largest follicles ranged between 2 and 8.5 mm. The nonpregnant animals up to April 8 numbered five. Three of the five had corpora lutea. Of the two remaining, M303 had one ovary lost, and M268 had a large corpus albicans (4 by 3 mm). The corpora lutea in the three nonpregnant seals measured, respectively, 6 by 5.5 mm (November 29), 9.5 by 5 mm (January 15), and 7 by 5.5 mm (January 16). All corpora lutea were regressing. Recent abortions might have occurred in the seals killed January 15 and 16. The size of the corpora lutea and the late date suggest this possibility. The four remaining 9 year olds collected between April 8 and June 27 all supported very active corpora lutea with an average size of 10 by 7 mm. All contained more than one corpus albicans. Follicular activity was low in comparison with the prepartum period of high activity.

Tenth Year. Eighteen seals composed the 10-year group. All were mature. The group taken between November and April was made up of seven pregnant and two nonpregnant animals. Specimen M181, collected on December 19, was not visibly pregnant and had an unusually large (10.5 by 7 mm) corpus luteum. An early abortion or a late ovulation is suggested. Specimen M585, collected on February 7, had no corpus luteum but several corpora albicantia. The mean corpus-luteum size in this group was 12 by 10 mm. The only twins recorded in the entire study were taken from a 10 year old, M615, on February 7. The fetuses were in both horns, and both ovaries contained corpora lutea. That on the right measured 17 by 11 mm, and that on the left, 15 by 5 mm. This suggests that ovulation had occurred nearly simultaneously in both ovaries.

Nine seals composed the group between April 8 and June 28. All but one contained corpora lutea. A date centering between May 15 and May 21 is suggested here as the approximate time when ovulation occurred. Specimen M1541, killed on May 19, supported a 2- by 2-mm corpus hemorrhagicum, and M1555, taken on May 21, held a recent corpus luteum measuring 8 by 7 mm.

The corpora albicantia averaged 1.5 per seal. The average size of the corpora lutea in this group was 10.9 by 7.4 mm. All appeared normal and functional.

The seal without the corpus luteum supported a large (11 by 3.5 mm) corpus albicans. It was collected June 18. It is probable that this specimen had been pregnant and that the corpus was that of the pregnancy. The large size of the corpora albicantia in many of the nonpregnant animals indicates probably that after parturition the size of the corpus is not affected as much as are the luteal cells. Several of the corpora albicantia compared in size to functional or regressing corpora lutea except that the luteal cells had lost their characteristic yellow color.

Eleventh Year. Twenty specimens made up the 11-year group. Fourteen were collected between November and April 8, and thirteen of them were pregnant. The nonpregnant seal supported a 6- by 6-mm corpus luteum; there were four corpora albicantia in the two ovaries. Six seals of this age were collected between April 8 and June 27. Five had corpora lutea. Specimens M1419 and M1452, collected on April 19 and 21, respectively, had regressing corpora lutea (10 by 8 mm and 7 by 5.5 mm). Specimens M2041 and M2098, collected on June 17 and 19, respectively, were supporting active corpora lutea (14 by 7 and 10 by 4 mm). The animal lacking a corpus luteum was collected on April 21 and had a large (4 by 3 mm) corpus albicans.

Twelfth Year Plus. An analysis of specimens in the 12^+-year group showed a pregnancy rate of approximately 85%, and the same general pattern of ovarian activity prevailed. In several of the very old (20^+ years) seals, ovaries occurred with little or no follicular activity. These were classified as senile. The exact ages at which the cessation of follicular activity occurs is difficult to determine with the present aging techniques.

The most abnormal ovaries were from a 20^+ year old, M200, collected on December 22. The left ovary contained one corpus albicans 5 by 4 mm in diameter; two large (5+ mm) follicles, the largest being 10.5 by 6 mm; two follicles in the 3 to 5 mm range; and four follicles in the 1 to 3 mm range. Also contained in the left ovary were two corpora lutea measuring 12 by 11 mm and 5 by 4 mm. The right ovary showed similar activity with three corpora albicantia (11 by 11, 5 by 5, and 3-mm line scar); two large 5^+-mm follicles, the largest being 10 by

6 mm; and two 1- to 3-mm follicles. In addition, the ovary supported a 6.5- by 4-mm corpus luteum.

REPRODUCTIVE CYCLE There was a striking conformity of the reproductive cycle in the population of ringed seals examined. In 1960 on April 8, we attempted to secure fresh specimens of "unborn young." We had seen many frozen specimens secured and held by the Eskimos prior to this, but not a single fetus was brought in after this date. Likewise in 1961, April 8 was the last date on which a pregnant female was taken.

PUPPING LAIRS There was a large population of pregnant females in the Cape Thompson area and no reason to suggest that they went elsewhere to pup. The Eskimos tell of pupping lairs rarely discovered—snow houses with a breathing hole in the ice. These are usually found where sea ice is piled up and irregular. None were reported during our studies. We were informed that occasionally, with proper conditions for travel on the melting spring ice, many fallen-in birth lairs can be found where it would have been impossible to discover them before the melting of the ice.

An examination was made of considerable sea-ice structure. There is much honeycombing and opportunity for large air spaces throughout the massive jumbles of rough ice, and it is possible that suitable pupping spots are abundant over wide areas near Cape Thompson.

MATING Mating usually takes place within the first month after parturition. The males were potent primarily before the end of March, as evidenced by our finding epididymides packed with sperm at that time. Pregnant females disappeared the last of March and first of April. The males remained potent until the first part of June, according to the microscopic appearance of the testes and epididymides. The corpus luteum of pregnancy regressed rapidly, and by about May 20 the new corpora lutea were found. This indicates that in most females ovulation (and presumably fertilization) had occurred before this date.

IMPLANTATION The fertilized ovum develops to the blastocyst stage and then is arrested for a period of about 3½ months (McLaren, 1958b). Implantation then occurs, and the development of the fetus begins. McLaren notes that he found the smallest fetus in mid-August, and he suggests that this had been implanted 1 to 2 weeks earlier.

We found no abnormal implantations in the Cape Thompson area, but a unique specimen, M2217, was sent to us from Barrow. This was an apparent abdominal pregnancy in which death of the fetus occurred at a late stage of development. This specimen was brought in to Gary J. Brusca on May 5, 1962, by Daniel and Clyde Okomailuk and Billy Ahlalook. It consisted of a 7-lb fetus, 24.5 in. long, lying in a thickened amniotic sac free in the peritoneal cavity. Inflammation with dilated vessels over the kidneys, swelling of the organs, and considerable peritoneal fluid was described grossly in the well-nourished female. There was extensive slippage and accumulations of lanugo hair. Microscopic examinations of several tissues showed recognizable structure with loss of cellular detail. The cyst wall contained considerable calcium; this was a beginning lithopedion. We judge this to be an excessively rare phenomenon in pinnipeds because of the presence of a tentorium around the ovary, which probably restricts movement of the ovum. Implantation is usually on the same side as the ovulation.

DEVELOPMENT OF FETUS Observations were made on 240 fetuses of the ringed seal collected at Point Hope (a few from Kivalina) in 1960-1961. The sex ratio was approximately equal: 113 males (49.14%) and 117 females (50.86%). No disparity of size of the fetuses was noted between the sexes.

The fetuses in November and early December varied from 173 to 287 mm in length and from 245 to 896 g in weight. In March and early April, the specimens varied from 512 to 660 mm in length and from 3.4 to 4.5 kg in weight.

No body hair except vibrissae and eyebrows was found on M49, collected on November 25. On the following day, however, a fetus with hair extending from the nose to the dorsum of the head was taken. On November 29 a fetus had hair extending from the nose to the scapular region. The mid-dorsal hair was 2 mm in maximum length. There is a progressive covering of the fetus with this lanugo hair, which is pure white and wooly and measures in the mid-dorsal area up to 50 mm in length. This fetus is the "unborn seal" used by the Eskimos for items of clothing. McLaren (1958b) substantiates other workers in stating that in the eastern Arctic the fetal coat begins to shed about 2 weeks after birth. We found that several of the fetuses obtained in late March and early April showed the darkening of the skin beginning the juvenile molt. There is a great tendency for the hairs of these late fetuses to be shed.

More than 50 fetus skulls were prepared for study. These showed the milk teeth to resorb completely before birth.

On May 17 and 21 two young-of-the-year weighed, respectively, 16 and 18 lb. These weights suggest a doubling in weight during the nursing period. The lengths were 640 and 602 mm, respectively, which indicates little increase in length. The blubber thickness, however, increased from a probable 4 mm thickness at birth to 11 mm.

According to McLaren (1958b), weaning takes place before or at the time of ice breakup. Lactation was found definitely in only two females, one on April 30 and the other on May 7. An interesting phenomenon was found on May 21, when a 44-lb male, judged to be a yearling, was taken with milk in its stomach.

Distribution and Migration

The essential general distribution of the ringed seal is polar and is limited more or less by the distribution of the ice. It is found in several land-locked lakes in Europe and North America. In the Bering Sea it extends as far south as St. Michael and Bristol Bay; on the Asiatic side this species extends to Hokkaido and the Sea of Okhotsk (Scheffer, 1958).

As with some other marine mammals, migration is not complete since a few individuals are regularly obtained in Bering Sea localities during the ice-free months. The relation of the population to the south on the Asiatic side is not clear at this time. If the movement of this population in the Bering Sea is similar to that on the Alaskan side, we must assume that it also migrates into the Arctic for the summer months. The seals in the Sea of Okhotsk, however, apparently remain here (Tikhomirov, 1961) and thus are analogous to populations of some other species of marine mammals, such as the gray whale and the bowhead whale, which complete their northward migration in the Sea of Okhotsk.

The Cape Thompson area is ideal for studying migratory phenomena of the ringed seal because of the large harvest there. Definite migration is evident; in the ice-free months there are no seals present. With the formation of ice in November (occasionally in October), seals are suddenly present, and they persist through June. Again in late June or July, there is a dramatic disappearance of seals until the next cycle is repeated. We have similar reports from other villages of the Arctic and Bering Sea; there appears to be little doubt that a mass migration of great numbers and over many hundreds of miles is the usual seasonal occurrence. It is likely that this large Bering Sea winter population is a direct southward migration of the summer arctic seals.

There are, in addition to the general migration, movements of populations. Table 2 shows the large differences in the makeup of the ringed seal harvest month by month and in shifts of adults compared to immatures and males to females. Whether or not this is a usual phenomenon every year we do not know. Certainly the great preponderance of immature specimens in the month of June is usual; these individuals are known as "spring seals" by the Eskimos. A studied examination of the catch during the ice months gives us the definite feeling that, although there may be static populations in the Cape Thompson area, there is a dynamic flow of seal groups. This is equalled by the ebb and flow of the ice, with its open leads, frozen packs, and drifting, moving ice fields. We believe that only by considerable long-term research on the seal populations and by correlation with oceanographic and meteorologic winter data will these phenomena be properly understood.

BIOLOGY OF THE BEARDED SEAL

Age and Sex Distribution by Month

Age determination is difficult in the bearded seal. The only recommended method for establishing age groups by year is to examine the claws for annual banding (McLaren, 1958a). Although our data tend to support this hypothesis, we do not consider the reliability satisfactory enough at the present time. Refinements of this or other methods should be made and are being investigated.

For our purposes we are classifying the bearded seal only as immature and adult. One hundred and seventy-three specimens had sufficient data for classification. In the female the criterion for determining adults was the formation of a corpus luteum or corpus albicans in the ovary. In the male the criterion was evidence of spermatogenesis in the testis and the size of the baculum. The general length and body weight were correlated with evidence of sexual activity (Table 12).

The bearded seal is usually absent from the general Cape Thompson area during the ice-free months. Occasional immature individuals are taken in the lower reaches of the Kukpuk River in the fall. We believe the fluctuations in abundance are primarily part of the mass migration with the ice edge. As with

Table 12—SUMMARY OF GROWTH OF TOTAL LENGTH, LENGTH OF BACULUM, AND WEIGHT OF TESTES OF 68 SPECIMENS OF BEARDED SEAL

Length of body, mm	Number of specimens	Weight of testis, g		No. of specimens* with indicated length of baculum, mm			
		Average	Extreme	<50 mm	50–74 mm	75–99 mm	100–151 mm
<1300	1	4		1			
1300–1399	0						
1400–1499	4	5.8	4–7	4			
1500–1599	5	7.6	5–13	4	1		
1600–1699	8	6.6	4–13	5	3		
1700–1799	6	16.8	12–23		6		
1800–1899	6	16.7	11–23	1	4		
1900–1999	4	19.5	13–29		2	2	
2000–2099	9	45.7	22–89			3	5
2100–2199	14	47.4	19–93			3	10
2200–2299	10	57.1	34–75			1	9
2300–2399	1	67					1

*Discrepancies in totals are due to lack of parts.

walrus and beluga, there are apparently residual populations to the south although concentrations of bearded seal are not found except during migration.

Table 1 shows the hunters' take during the winter of 1960-1961. The ugruk (bearded seal) is always a desirable catch, and hunters go to considerable effort to secure one; thus, the table probably represents rather accurately the relative abundance during the winter and spring. Shot animals tend to sink even in midwinter; so the loss ratio is probably greater than that for the ringed seal. The Eskimos state that pregnant females are likely to float. This may give the bias noted on Table 2 (for adult females over adult males) in the small series available. Immature seals make up the larger proportion in the winter months; the entire catch of this species is, however, spotty until June. At this time there is an almost two for one preponderance of adult females over adult males and a definite preponderance of adults over immature specimens.

Size and Growth

Two specimens indicate the size at birth. A male fetus (MLJ4075) at term on Apr. 21, 1960, weighed 74 lb and was 1310 mm long. A male pup (M1474) taken May 4, 1961, weighed 67 lb and was 1275 mm in length.

The sizes of the adults were approximately equal. A sample of 20 consecutive adult males and 20 consecutive adult females taken June 17 to 19, 1961, showed an approximate 4% greater total length in the females. They ranged from 2000 to 2370 mm, the average length being 2224.6 mm. The males ranged from 1982 to 2330 mm and averaged 2160.4 mm in total length. It was not possible to secure weights on the larger animals; one female (M1374) weighed 793 lb, with no allowance for blood and body fluids spilled.

Food Habits

The stomachs from 164 bearded seals collected from the middle of November 1960 to the middle of June 1961 at Point Hope and from 29 bearded seals collected in February, April, and June 1960 at Kivalina were available for comparative examination. The results of the examination appear in Tables 7 and 8. The classification list of fishes and invertebrates that were found in stomachs of ringed and bearded seals shows the species that were identified. A description of the collection area and laboratory methods is included in the section on ringed seal.

The bearded seals apparently could reach the bottom to feed and had the same opportunities for obtaining food that the ringed seals had; however, they fed on the slower moving and sedentary food species.

There appeared to be no significant difference in feeding habits between sexes. An analysis of feeding habits by year class, age group, or locality was not made. There is undoubtedly local variation in food species taken because of the bearded seal habit of feeding on sedentary bottom dwellers whose distribution over the ocean floor is irregular. There were no significant differences between the food species found in stomachs from Point Hope or Kivalina.

More than 50% of the bearded seal stomachs examined contained pebbles (up to 30 mm), sand, or gravel; and in one instance mud was found. Stomachs contained the largest amounts of this material in June when the seals were feeding extensively on clams. More than half the stomach contents of one specimen was sand and gravel. The high incidence of inorganic matter in bearded seal stomachs was to be expected in animals that feed to a great extent on bottom-dwelling forms.

The stomach contents of individual seals exhibited greater variety than did those of the ringed seals. Only a few stomachs were examined in which the contents consisted entirely of one food species. Although there were only six stomachs collected during December, January, and February, the bearded seals, presumably having the same opportunities as the ringed seals, failed to take arctic cod in appreciable amounts. This could be an indication of food preference. Food preference was possibly indicated again in June when clams formed a large part of the diet.

Variety in the contents of a bearded seal stomach was illustrated by a stomach collected Mar. 11, 1961. The stomach contained 5 sand lance (*Ammodytes hexapterus*), 12 shrimp (*Crangonidae*), 8 shrimp (*Sclerocrangon boreas*), 2 shrimp (*Lebbeus groenlandicus*), 1 crab (*Brachyura*), and 11 hermit crabs (*Pagurus brandti*). Apparently the seal took whatever he could find on the bottom and on his way to and from the bottom.

Although the sample size was small for some months, it would appear that the average volume of stomach contents reached a peak in February and then gradually dropped until the end of the study period in June. No abrupt drop in volume comparable to that observed in the ringed seal during this same period was apparent.

Changes occurred in numbers and variety of food species during the collection period. These changes might be due to several factors, including availability, abundance, and preference. An indication of availability might be interpreted by the sudden appearance in stomachs in June of large numbers of clams (*Pelecypoda*). One possible explanation for this could have been a shift in the ice or the opening of a lead, making available clam beds that had not previously been open to the seals. Seasonal changes in the abundance of the various food species also occurred. The percentages of the total volume of major food species by month are

November: shrimp, 60%
January: shrimp, 85%
February: shrimp, 52%; arctic cod, 24%
March: hermit crabs, 56%; shrimp, 25%
April: shrimp, 51%; crabs (Brachyura), 14%
May: shrimp, 27%; crabs, 24%; unidentified decapods, 23%
June: clams, 38%; crabs, 24%; and shrimp, 13%

Fish were of relatively minor importance as food for the bearded seals. As would be expected in a bottom-feeding animal, the few fish that were present were primarily benthic types. In February, the only month when an appreciable amount of fish was present in the stomachs, arctic cod formed 24% of the total stomach volume. In contrast, arctic cod at this same time formed 90% of the total stomach volume of the ringed seal.

Shrimp were of major importance in the diet of the bearded seals throughout the study period. The families Hippolytidae and Crangonidae were present in all months. Shrimp of the family Pandalidae were present in the collection during all months but November, when only one stomach was collected. The large shrimp *(Sclerocrangon boreas)* was identified in more stomachs than any other species. *Lebbeus groenlandicus* was identified in six of the seven collection months. *Argis lar* was identified in five of the seven months. *Pandalus goniurus* appeared in four monthly collections. Nine species of shrimp were identified from stomachs of bearded seals.

Hermit crabs were present in collections from all months. In March, when they formed 56% of the total stomach volume, they were found in three of the six stomachs collected. Crabs were well represented in the collection; they formed major parts of the food species in April, May, and June. However, in most instances only the abdomens appeared in the stomachs. An unidentifiable species of gastropod was present in two stomachs collected in June. No shells were found, but 171 operculums were counted in one stomach. Unidentified clams were major food species in June and were found in 35 stomachs. In one individual 183 clams were counted. No shells were present in any of the stomachs; clam feet and siphons were the countable parts present.

Many other species were identified one or more times in the collection, but their occurrence here is thought to be accidental. Hydractinia colonies were present on shells. The large amount of sponge (Porifera) in the June collection is of interest. From the amount taken, almost 2000 cm^3 in six stomachs, it would appear that the sponges were taken deliberately rather than accidentally. Leeches (Hirudinea) were identified in four stomachs. MacGinitie (1955) mentions that the only species of leech he obtained at Point Barrow was a specific parasite of the shrimp *(S. boreas)*, which occurred commonly in our collection.

Reproduction

Bearded seals were usually born in the last part of April. The Eskimos state that during whaling season they occasionally have seen mothers and young ugruk on the ice. We have seven specimens of fetuses taken during the months January through April (Table 13).

The fetal coat of the bearded seal is a crinkly dense black to dark-brown hair; the texture of the hair is much the same as that of the ringed seal but denser. Several specimens show light, nearly white patches dorsally without differences in texture. In the two specimens taken in early April, coarse straight fur was replacing the lanugo (fetal) hair but could be seen only by spreading the fur.

Table 13—WEIGHTS AND LENGTHS OF SEVEN BEARDED SEAL FETUSES COLLECTED AT POINT HOPE, 1960–1961

Specimen No.	Date collected	Sex	Weight, lb	Length, mm
M363	Jan. 17, 1961	Female	18	680
MLJ4076a	January 1960	Male		
M664	Feb. 10, 1961	Female	42	982
M1095	Mar. 1, 1961	Male	45	1005
M1370	Apr. 7, 1961	Male	76	1228
M1375	Apr. 8, 1961	Female	56	1170
MLJ4075	Apr. 21, 1960	Male	74	1310

A fetus taken on April 21 had completely shed its fetal hair and was uniformly covered with its short straight first molt. This animal must have been almost at term because, on being removed from its mother, it was so lively it had to be killed. We have only one pup of the year (M1474), which was secured on May 4, 1961. This was a male that weighed 67 lb and was 1272 mm long. In comparison with the April 21 specimen, its pelage was slightly longer and more uniformly silver gray, without the considerable mottling present on the fetus.

According to previous research the female bearded seal breeds only every other year. The age of onset of breeding is 6 years in the female and 7 years in the male. Delayed implantation after about 2½ months apparently occurs (MacLaren 1958a). Without more confidence in our aging techniques, we are in no position to verify these observations. During the months January through April, we examined six adult female bearded seals; five of them were pregnant.

Table 12 shows the development of sexual characteristics in 68 male specimens. It appears that the length of the animal is well correlated with a progressive growth of the baculum and with increase in size of the testis. The evidence of maturity occurs in the 2000-mm-total-length category. Several of the Eskimos have described a dwarf group of ugruks, occurring particularly in the Kotzebue area, called "ugruchats." Some of the natives consider these fully mature animals; others say that they are the young ugruk. From the data at hand, we find no evidence of dwarfing among the adult animals and thus at present consider "ugruchats" as immature seals.

Distribution and Migration

The general distribution of the bearded seal is "circumboreal at the edge of ice" (Scheffer, 1958). It ranges as far south as Bristol Bay, Alaska, and northern Hokkaido and the Sea of Okhotsk. It appears to be intensely migratory and associated with the ice edge although individuals may be found throughout its range during the ice-free months (compare with other marine mammals such as the walrus and beluga).

The bearded seal is generally scattered in the Cape Thompson region except during the northward spring migration. Of the 173 bearded seals cataloged at Point Hope in 1961, 92 were recorded during the 3 days June 17 to 19, and an additional number that could not be examined were secured at this time. Whether herding occurs during the southward migration in the fall, as it does in walrus and harbor seal, is not known. Although the sample is small, there is a suggestion of early northward migration of adult males in May. The total picture of migration and local movements related to age groups and sex is a largely unknown entity that deserves further study.

REVIEW OF SPECIES OCCURRING IN CHUKCHI SEA OTHER THAN RINGED AND BEARDED SEALS

Except for the ringed and bearded seals, no species was collected in sufficient quantity for biological analyses. We have brought together the available information on other species to give a reasonable picture of each one. The treatment is irregular according to what is judged to be of importance in this chapter.

Not all the species discussed have been observed in the immediate Cape Thompson area; however, all have been reported in the Arctic Ocean.

Walrus

In the study area the walrus is essentially an animal of the edge of the ice pack. The general migration picture may be pieced together thus: During the maximum advance of the ice pack in March and April, large numbers of walrus (70,000 estimated) are scattered over the Bering Sea (Kenyon, 1960). Large numbers pass by St. Lawrence Island and particularly the Bering Strait in spring and again in the fall as the ice boundary moves with the seasons. Some animals, probably predominantly males, remain in the Bering Sea in the summer. Summer stragglers are occasionally present in the general Cape Thompson area, and small groups occur rarely.

According to the hunting records, it appears probable that the main migration route of the walrus is out beyond the usual hunting area of the Eskimos at Point Hope and Kivalina, but a few are regularly obtained. Likewise some walruses may frequent the ice pack along the open leads during the entire winter. These are occasionally available to the hunters, as in the winter of 1959-1960. On Nov. 6 and 7, 1960, a southward migration of several hundred was visible from the plane off Point Hope. Walruses were audible from the beach at Point Hope during the ensuing week. Ice conditions prevented hunting.

The published records (Nelson and True, 1887; Bailey, 1948; Brooks, 1954; Scheffer, 1958) indicate clearly that the summer distribution is spread out along the ice edge from about 170°W east to beyond Point Barrow. On either extremity of this distribution, walruses occur rarely. Except for unusual distribution records, the ranges of the Atlantic and Pacific walruses do not meet; this is primarily a function of the ice conditions. Certainly there is no opportunity for any significant populations to be in contact during the breeding season, which is reputed to be in May. A single calf is born on the ice in April or May (Nelson and True, 1887). These animals are gregarious and occur in herds or "pods." They are bottom feeders, which limits their general distribution to relatively shallow seas.

Economically the walrus is of moderate importance to the Point Hope Eskimos because it supplies ivory for carving and meat for dog food.

Harbor Seal

In the Arctic the harbor seal is better known as the spotted seal. Its distribution is general, and probably it is common on the floating ice in June. It regularly occurs during the summer in scattered numbers, particularly around river mouths. It is rarely taken in the Cape Thompson area during the ice-fast months, although Nelson and True (1887) state that it is resident wherever found. Concentrations in the fall have frequently been reported. This phenomenon occurs regularly in the Kukpuk estuary a few miles north of Point Hope. It is evident that the harbor seal is strongly migratory in this part of the Arctic and responds to the advance and recession of the ice pack.

The harbor seal is reported to have its single young on the ice in April or May (Nelson and True, 1887). It probably subsists largely on bottom fish.

Economically the harbor seal is not of great importance in the Cape Thompson area. The hide is the part most used by the Eskimos. The meat is less palatable than that of the ringed seal but is eaten by some people and is used for dog food.

Ribbon Seal

The ribbon seal is primarily of eastern Arctic distribution and ranges from the Sea of Okhotsk into the Siberian Arctic Ocean. It apparently migrates with the floating ice much as does the walrus and must be classified as of casual occurrence in North American waters. References to concentrations of this species have been made by summer travelers into Siberian waters (Nelson and True, 1887; Borden, 1928).

According to Tikhomirov (1961), the young are born in April and molt shortly thereafter in the Sea of Okhotsk. Aggregations of nursing individuals are related to the central ice sheet in the western and northern parts of the sea. Although statements are made about the departure of ribbon seals from the Okhotsk Sea, it is not yet documented that this population migrates northward through the Bering Sea and into the Arctic Ocean.

In the Cape Thompson area, there are records of ribbon seals each year from Point Hope and occasionally from Kivalina. Most occurrences here are in June during the northward migration; occasionally specimens are secured in November. This species must be involved in mass or herd migration. Specimens obtained from St. Lawrence Island are grouped strongly. In 1961 five specimens were taken over a 4-day period at Point Hope. Three were adult females, and two were adult males. A single specimen taken in November 1959 was an adult male. In all cases the stomachs were empty of food.

Fur Seal

The normal northern limit of the fur seal is approximately their summer breeding ground on the Pribilof Islands. In the winter months they spread out over the North Pacific, and some go as far south as Mexican waters. Individual wanderers have penetrated into the Arctic as far as Letty Harbour, Northwest Territories (Maher, 1960). The fur seal was, however, apparently unknown at Point Hope until the summer of 1960, when two specimens were secured. In the summer of 1961, one specimen was taken.

Beluga or White Whale

The beluga, or white whale, is a common species with definite migratory habits. Ordinarily it first appears in the open leads at Kivalina and Point Hope in early April before the great black (bowhead) whales appear. In 1960, however, no belugas were seen until after the bowhead whales began passing by; this was the first time this had happened in the memory of the hunters in the Point Hope–Kivalina area.

Belugas apparently remain in the Arctic as far east as the MacKenzie River until ice formation forces them south again. As with other arctic marine mammals, all individuals do not migrate. Summer populations are recorded as far south as Bristol Bay.

Belugas, defintely gregarious, occur in groups of up to a hundred individuals and are well known for their habit of ascending freshwater streams. Nelson and True (1887) state that they are found more commonly in the shallow water of the Alaskan coast than in the deeper waters of Siberia.

The young are produced singly about the middle of June (Nelson and True, 1887). A fetus weighing 50 lb and measuring 1240 mm was secured on Apr. 21, 1962. This is considerably smaller than data cited by Tomilin (1957) for Greenland specimens in April.

Two stomachs were examined from specimens taken in May 1961. They contained arctic cod and shrimp of at least three species. These are the food items of major importance to the seals in this area also.

The beluga is of considerable importance for food and for sinews for sewing in the Cape Thompson area.

Narwhal

The narwhal has not been reported from the Chukchi Sea, but Geist, Buckley, and Manville (1960) report two specimens from the Bering Sea. This indicates that individuals may wander beyond their usual range (westward to Barrow from the eastern Arctic). Old tusks occasionally obtained at Wainwright suggest that this species formerly was more abundant in the western Arctic.

The narwhal is reported to migrate in large herds in the eastern Arctic and to feed on fish and shrimp. The tusk, which may reach 9 ft in length, is the left upper canine tooth; there are no other functional teeth.

Pacific Killer Whale

The Pacific killer whale, with its characteristic high dorsal fin, is reported from the Eskimo villages north to Barrow, including Kivalina and Point Hope. No utilization is adequately reported from any area. Several Eskimos stated that these whales are fierce and dangerous, but we have no firsthand report of attacks on boats.

The predatory proclivities of killer whales against other marine mammals of all species are well documented.

Harbor Porpoise

The small (less than 6 ft) harbor porpoise is regularly recorded from as far east as Barrow (Bee and Hall, 1956) and the Chukchi Sea (Tomilin, 1957). It is a common species in more southern waters but has not been reported from the immediate Cape Thompson area.

Gray Whale

The gray whale, as the bowhead, is protected from commercial whaling by international agreement. The gray whale is well known for its remarkable migration. It has been publicized in the past few years because it concentrates along the California coast where accurate censusing may be done. From November to May it formerly was found in the lagoons and along the coast of California and Baja California (Scammon, 1874). Gradually it was restricted to the coast of Baja California, Sonora, and Sinaloa (Hall and Kelson, 1959), where calving occurs. The migration path fans out above the California coast, some individuals continuing along the coast and others at sea. During the summer months it is found in widely scattered areas of the North Pacific, Bering Sea, and Arctic Ocean. There is also a Korean population that has similar migration patterns, but it probably goes into the Sea of Okhotsk. It is not known if these two herds mingle.

A number of observations identify the gray whale in the Cape Thompson region. During oceanographic surveys in August, 1959, Ford Wilke on the *John Cobb* saw many gray whales bottom feeding. Several strandings have occurred near Cape Thompson. Bailey and Hendee (1926) state: "These whales are occasionally seen in the Arctic in summer . . . One or two were seen from the beach at Wainwright . . . ."

We do not know when these whales leave the Chukchi Sea, but Scammon (1874) states that they appear on the Oregon coast in October and November. Since their arrival in California is as late as February, it is possible that the departure could be as late as October.

To our knowledge Point Hope people have not hunted the gray whale. In the years 1954 to 1959 during the months of July, August, and September, one gray whale had been killed at Wainwright, and nine had been killed at Barrow. Most of these were young animals, but several were lactating females (Maher, 1960).

The original population of the California gray whale was estimated at "not over 30,000" (Scammon, 1874). It is now estimated at between 8000 and 9000 (Rice, 1961).

Finback Whale

The finback, a baleen whale, is streamlined and speedy and may reach a length of 80 ft. It has been reported from the western Chukchi Sea (Borden, 1928;

Tomilin, 1957). It has a worldwide distribution and is commercially widely utilized. It feeds on crustaceans and fish.

It is marked by numerous well-defined throat grooves and a moderate-sized dorsal fin posteriorly.

Sei Whale

The sei whale is a smaller, somewhat chunkier edition of the finback whale and has been reported from the eastern Chukchi Sea (Tomilin, 1957). It differs from the common finback in having less than 340 major baleen plates, which are blackish (not purple and white as in the finback whale), and in having the ventral surface of the flukes dark blue to brown instead of white. The general distribution is worldwide. It feeds on plankton.

Little Piked Whale

Reported from the Chukchi Sea by Scammon (1874) and Tomilin (1957), the little piked whale is similar in general form and character to the other fin-backed whales but is less than 33 ft long. The white to yellowish-white baleen is short (less than 10 in.). A characteristic marking is a broad white band crossing the upper side of the foreflipper. It feeds on fish.

Humpback Whale

The humpback whale is a cetacean of worldwide distribution which ranges into the Chukchi Sea in the summer (Tomilin, 1957). The thickset body, not over 50 ft long, and long foreflippers give a characteristic form to the animal. It feeds primarily on shrimplike crustaceans.

Bowhead Whale

The bowhead whale and the Pacific right whale are protected from commercial whaling by international agreement. The general distribution is Arctic, both Atlantic and Pacific. It is rarely found far from the ice and occurs with regularity well under the pack. It regularly passes the Cape Thompson area in April when the southern limit of the pack is many hundred miles south of Bering Strait. There is evidence of passage from the Atlantic to the Pacific Arctic in the finding of a British harpoon in a whale killed in the Kotzebue area in 1880 (Nelson and True, 1887).

The bowhead whale was the major species secured by the great arctic whaling fleets between 1848 (Scammon, 1874) and 1908 (Brower, 1954). During the latter years the numbers were greatly depleted, and all commercial hunting finally stopped because of the drop in the price of baleen.

It may be assumed from present fragmentary observations of these whales that a reasonably large population now exists. The total yearly kill in Alaskan waters by the Eskimos probably never exceeds 30 to 40 animals, including those killed and lost. Whaling is now done at St. Lawrence Island, Point Hope, Wainwright, and Point Barrow. In the days of extensive commercial whaling, the harvest of whales was many times the kill taken over the last 60 years.

We can piece together bits of information to get a reasonable idea of the general migration cycle. The population in the Sea of Okhotsk is probably separate since bowhead whales remain there after the ice has melted. Bowhead whales are not seen south of the southern edge of the ice pack in the Bering Sea (Scammon, 1874). Kenyon, in extensive surveys for walrus in 1960, saw only one whale in this area. Bowhead whales may first appear at Kivalina and Point Hope as early as the end of March. They are regularly present in April, through May, and occasionally into June. All movement of the whales is toward the west, parallel with the south shore, and it is assumed that these whales turn north to pass Point Lay, Wainwright, and Barrow. In 1960 we received an unconfirmed report that a whale was seen at Barrow on April 15; the first whales were seen at Point Hope on April 11. The first whale was struck but not secured on April 15. On Apr. 13, 1961, three bowhead whales were sighted. The first whale was struck on April 29. Bailey and Hendee (1926) and Bailey (1948) report that in 1922 the first whales passed the Bering Strait on April 13, a few days before they appeared at Wainwright. Hendee (1930) stated that the whaling teams were out from May 1 until June 15. Rainey (1945) reports that at Point Hope the whales had appeared in late March or early April and had passed by early in June. Murdoch (1892) states that at Barrow the bowhead whales travel along the leads of open water from the middle of April to the latter part of June in large numbers and return about the end of August. Brower (1954) states that the dates of the native whaling season at Barrow are usually in April and May. The fall return migration is generally unnoticed in the Cape Thompson region, which may be an indication of an offshore passage. Don Foote, in the fall of 1960, observed westward-moving whales (not identified) on the north shore near Point Hope.

We examined three bowhead whale specimens. Specimen M39 was a young male 30 ft long, which was taken Apr. 18, 1960. The testis measured 9 in. in diameter. The stomach was empty. Specimen M1527 was a young female 26 ft long, which was taken May 13, 1961. The stomach was nearly empty, containing fragmentary remains of Polychaeta, Reptantia, Gastropods, Crustacea, Echinoidea, and sand and gravel. The ovaries had a maximum diameter of 190 mm and were immature. Specimen M1571 was a lactating female 46½ ft long. The ovaries had a maximum diameter of 330 mm; one ovary contained a corpus luteum 83 by 45 mm, and the other, a degenerative corpus luteum 47 by 21 mm. The stomach was empty.

The following two generalizations are probably true: Migrating whales do little feeding, and most of the catch of the Eskimos consists of immature individuals.

The prestige of the hunt and more particularly of the capture must be seriously considered in regarding the pattern of utilization of the bowhead whale in the Cape Thompson area. At Point Hope there were 13 whaling crews during the period of our study. Usually each crew has approximately eight men, all of whom may not be present on the ice at one time. A woman or girl cook and some older boys may be part of the camp crew. When all the crews are out on the ice, it is possible that as many as 130 persons are away from the village for the length of the stay on the ice. This maximum figure is probably seldom realized. If the whaling season lasts as long as 6 weeks or more, considerable time and effort of the village goes into this activity. In addition, before the season considerabl time is expended in carving paddles, making bleached ugruk skin boats, anc preparing the seal-poke floats, lines, harpoons, bombs, and other necessar paraphernalia. If a whale is secured, most of the able-bodied villagers go out on the ice to assist in processing it or simply to enjoy the excitement.

During the time of whaling, the hunters also secure ringed seals, bearded seals, and belugas.

Traditionally, when a whale is secured, eight teams get a share according to the order in which they reach the struck whale (Rainey, 1945). In 1959, when only one whale was secured, the effort was obviously inefficient from the man-hour point of view. In 1960, when four whales were secured, the economy was better justified. In 1961, two whales were secured. However, for these traditionally whale-hunting and proud people, to consider only the economy of the situation would show a lack of perspective on our part.

The alternative for whale hunting is caribou and ringed and bearded seal hunting, and the returns are greater for the effort spent on these species.

An interesting correlation of migratory patterns is noted here. Bailey and Hendee (1926) quote the Eskimos at Wainwright as stating, "The first living creatures to appear in the spring are the gulls, the second the white whales . . . , the third, the bowhead . . . , all three arriving ahead of the eider ducks." (Actually at Point Hope there are seabirds out on the open leads all winter.) Bailey (1948) further specifies that no two years are alike in the Arctic but that, when the first white-winged gulls appear along the coast in early spring, the Eskimos know that soon the great bowhead whales will be working the open leads.

Rainey (1945) states that in late March or early April the snowbirds arrive and whales follow (the beluga first and then the large whales).

In 1960 we first saw snow buntings on April 9. The Eskimos told us that they had been present for 2 days. On April 11 the first whales were sighted far out on a large area of open water. Gulls were first seen by us on April 22 although they might have been present earlier. Belugas, however, did not arrive until later. This was the first time in the memory of the hunters that the belugas did not arrive before the big whales; this unusual occurrence was noted in Kivalina as well as Point Hope. In 1961 belugas were first sighted on April 10, and the bowheads, on April 13.

Polar Bear

Approximately 18 polar bears were secured by the native hunters in 1959-1960, and 3 were taken in 1960-1961. One bear was shot near Kivalina in 1960. After the airplane hunters began to fly in February, few bears (none in 1960 and 1 in 1961) were taken by the Eskimos. The question has been raised that increased airplane hunting destroys or herds the bears before they arrive in the Eskimo hunting area. Whether or not there will be a place for airplane hunting in harvesting otherwise untapped populations remains to be biologically proved. The evidence at hand indicates that populations now are greatly reduced in numbers, particularly below Bering Strait, where formerly they were abundant (Nelson and True, 1887). Competent biologists are studying this problem and should have information pertaining to it within the next few years.

Polar bears may occur at any time during the ice season but are more common in the winter months. Hunting results showed that the density of the population is extremely irregular.

What is probably the largest bear of any species ever collected was taken in the Chukchi Sea on Mar. 3, 1961. It was shot north of the Diomede Islands by Arthur Dubs when he was flying out of Kotzebue. Approximately eight bears were seen in the 5 days of flying before this large specimen was sighted. The bulk and measurements of the skin and the size of the skull make it likely that this specimen far exceeds the 1700-lb polar bear from James Bay, Canada, a specimen now at the Carnegie Museum.

INTERNAL PARASITES OF MARINE MAMMALS

The collection of parasitic helminths was incidental to other work since it was impossible to undertake the careful dissections necessary for complete examination of the marine mammals. Much of the available material was taken from stomachs preserved for the food-habit investigations, but some specimens were collected from other organs. Although a detailed study of the helminths has not been completed, several species have been identified. These are listed here by host.

Bearded Seal

Phocanema decipiens (Krabbe, 1878) was the common helminth collected from bearded seals. Many specimens were found in the stomachs, and some were taken also from the duodenum. It occurs in several species of marine mammals, and infection results when fishes containing the larvae are eaten. Immature stages of *Phocanema* were commonly represented in the available material from preserved stomachs.

Although bearded seals often harbor cestodes, comparatively few were included in this material. Because its scolex is usually attached to the gastric mucosa of the seal, *Pyramicocephalus phocarum* (Fabricus, 1780) was found in many stomachs. Although its larvae occur in various species of cods and sculpins, the adult cestode exhibits a high degree of host specificity. A small cestode, *Diphyllobothrium schistochilus* (Germanos, 1895), was collected from the intestine of one animal. Two additional species of *Diphyllobothrium, D. cordatum* (Leuckart, 1863) and *D. lanceolatum* (Krabbe, 1865), both common parasites of bearded seals, were not recorded; they perhaps escaped detection because of their typical localization in the more posterior portions of the intestine.

Only one trematode, *Orthosplanchnus arcticus* Odhner, 1905, was recorded. It inhabits the gall bladder and bile ducts and sometimes the pancreatic ducts. The life cycle is unknown.

Ringed Seal

Larval ascarids of the genus *Contracaecum*, probably *C. osculatum* (Rudolphi, 1802), were often found in ringed seals and were usually attached to the stomach wall. This is another species of nematode that occurs in various pinnipeds. *Phocanema decipiens* was also recorded from the ringed seal.

Acanthocephalans of the genus *Corynosoma* were collected from one of the ringed seals examined. These parasites occur in various species of marine mammals and usually inhabit the lower intestine. A campulid trematode, not yet identified, was found in the bile ducts of one seal.

Harbor Seal

Unidentified ascarids were collected from a harbor seal. Both *Phocanema decipiens* and *Contracaecum osculatum* have been recorded from this host in the Alaskan waters.

White Whale

Nematodes of large size, as yet unidentified, were found in a white whale. The species *Stenurus pallasii* (van Beneden, 1870) has previously been recorded from this mammal in arctic waters. A large trematode, *Odhneriella seymouri* (Price, 1932), is found rather commonly in the intestine of this whale and presumably was overlooked in the present survey.

Polar Bear

The larvae of *Trichinella spiralis* Owen, 1835, were observed in the musculature of one bear. This is a common parasite of polar bears, and the rate of infection increases with the age of the host. Ascarids *(Contracaecum)* have been found in polar bears in arctic Alaska but are found only rarely. Few species of helminths are known to occur in this mammal.

SUMMARY

The marine mammals are the most important natural resource for the Eskimos at Point Hope and Kivalina. Six species of pinnipeds, two of cetaceans, and one of carnivore (the polar bear) were collected during this study. The ringed seal and the bearded seal occurred in sufficient numbers for biological analysis.

On census flights most seals were observed within a few miles from shore. Maximum concentrations occurred south rather than north of Point Hope. The average number of seals observed was 32 per 100 square miles, and the range was 1 to 237.

Data were collected from 2028 ringed seals obtained from November through June. The sex ratio was equal in fetuses, but males were predominant in the hunter's catch. Marked fluctuations of numbers and mature–immature ratios occurred. Pups are born in late March, and the birth weight is about 9 lb. Adult males reach a weight of about 225 lb and are slightly larger than the females. Food is primarily arctic cod in the winter and invertebrates in the spring. Breeding is in April and May; 86.7% of mature females are pregnant.

Data on 208 bearded seals were obtained. There was a preponderance of adult females; 80% of the total catch of the year was in June. A completely molted, ap-

proximately 70-lb fetus is usually born in late April and measures about 1300 mm in length. Adults weigh up to 800 lb and are up to 2300 mm long; both sexes are equal in size. Food is principally invertebrates.

All species of marine mammals in the area investigated are migratory. Their migration is related to the ice conditions.

Our specimens and data are subject to considerably more analysis than was possible for this chapter, and such analyses are being carried on.

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A NEW RECORD OF *PSEUDODIAPTOMUS MARINUS* SATO (COPEPODA, CALANOIDA) FROM BRACKISH WATERS OF HAWAII

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Sato (1913) originally described both sexes of *Pseudodiaptomus marinus* from warm neritic waters of Oshoro and Takashima, Hokkaido, Japan. Anraku (1953) again reported it from Oshoro. No other records of the species are known to me.

Plankton samples collected in 1964 and 1965 by the Department of Microbiology, University of Hawaii, from the Ala Wai Canal, Oahu, Hawaii, contained abundant examples of both sexes of a form which appears to be identical with

P. marinus. Its maximum concentration was at a station near the inland end of the canal, about 1.5 miles from the mouth, which empties into Ala Wai Yacht Harbor. The salinity at that station was about $18^0/_{00}$. The distribution of the species in other brackish-water areas in Hawaii is not known.

Material has been deposited in the United States National Museum (USNM 112647: six males, 0.94 mm to 1.01 mm total length; five females, 1.08 mm to 1.31 mm total length).

Most of the species of *Pseudodiaptomus* inhabit fresh or brackish water; those which live in the sea are considered to be neritic rather than oceanic forms. The occurrence in Japan and Hawaii of a neritic species is of interest from the standpoint of determining distributional and evolutionary pathways (Johnson, 1964). Other records of the genus from Pacific oceanic islands include those of Mori (1942), who found *P. clevei* A. Scott and *P. serricaudatus* (T. Scott) in Palau, and Grice (1964), who described a new species, *P. galapagensis,* from the Galápagos Islands. That species is very similar to the recently described *P. wrighti* Johnson (cf. Johnson, 1964) from the Pacific coasts of Mexico, Costa Rica, and Ecuador.

These and other species have been found in neritic marine waters and it is not unreasonable to assume that individuals could survive the salinity of the open ocean. For *P. marinus,* however, the distance between Japan and Hawaii would appear to require survival during several generations because the time required for transport by currents must be longer than the life span of any individual.

The remote possibility exists that *P. marinus* has been transported from Japan to Hawaii in ballast or other vessel water tanks. Until its life history is known, consideration of modes of transport, natural or otherwise, amounts to little more than speculation.

I thank Dr. George W. Chu of the Department of Microbiology, University of Hawaii, and his aid, Mr. Melvin Tanaka, for the opportunity to examine the plankton samples from the Ala Wai Canal, and Dr. Sigeru Motoda and Mr. Y. Morioka of the Faculty of Fisheries, Hokkaido University, for providing me with an excellent translation and figures of Sato's description of *P. marinus.*

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Forty-first Annual Meeting, 1965-1966, p. 18

Abstract

2. Use of a Submarine to Survey Populations of Planktonic and Demersal Invertebrates

Observations were made of planktonic and demersal invertebrates in waters off Barber's Point, Oahu, in September and October 1965, from the portholes of the submarine *Asherah*.

From visual observations of particle sizes and frequencies, an estimate of 1,000 mg of plankton per cubic meter of water was made; this is about 50 times the average volume of zooplankton obtained in net tows around Hawaii. Most of the particles were organic debris or non-swimming forms such as radiolarians. Little change in the amount of plankton was seen between the surface and 630 ft or from day to day. By way of contrast, observations from the bow chamber of the research vessel *Townsend Cromwell* in November 1964, in the area between Hawaii and lat. 10° N, resulted in estimated volumes of planktonic radiolarian colonies and ctenophores up to 250,000 mg and 30,000 mg, respectively, per cubic meter of water viewed. The larger portholes and 12-knot speed of the *Townsend Cromwell*, which allowed the viewing of an enormous volume of water per hr, and the depth-range of the *Asherah* are attributes which, if combined, would give a valuable tool for plankton research.

From observations of demersal invertebrates, general distribution patterns were determined. On the steep cliff face, at depths from 350-630 ft, the urchin *Chondreocidarus gigantea* was common, and the starfish *Linckia* sp. and unidentified hydroids were rare. At the top of the cliff, several thousand large spatangoid urchins were seen in densities up to 6 or 8 per square meter. At depths from 200-400 ft, large beds of pen shells, *Atrina vexillum*, were seen in densities up to 400 per square meter. Other invertebrates seen in or on the sandy flats were sponges, brittle stars (at night), tube worms, and cone shells. Trails and diggings of buried forms were common.

In depths from 100-200 ft, loose clumps of sponges 4-8 in. in diameter were seen in densities up to 10 per square meter. On rocks, clumps of unidentified bryozoans and soft corals as well as the urchin, *Diadema* sp., were seen. The stony coral, *Porites* sp., was scarce but was seen down to 350 ft. Large spiny lobsters were abundant at 250 ft and were seen down to 360 ft. The cleaning shrimp, *Stenopus hispidus*, was seen among rocks at 180 ft.

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THE ICITA ONE-METER PLANKTON NET: DESCRIPTION AND EVALUATION

by Jack W. Jossi

THE ICITA ONE-METER PLANKTON NET: DESCRIPTION AND EVALUATION[1]

The ICITA net is a 1-m plankton sampler designed by Mr. William C. Schroeder[2] for use during the Equalant cruises of the International Cooperative Investigations of the Tropical Atlantic (Austin 1963). By late 1966, more than 1,500 plankton samples had been collected with this net by the 19 vessels participating in the investigations, and by the Bureau of Commercial Fisheries *RV Geronimo* and *RV Undaunted* during subsequent cruises to the tropical Atlantic Ocean. Hydrodynamic characteristics of the net have been described by Mahnken and Jossi (in press). Because of the large number of samples taken and the international use of the net, a detailed description seems appropriate.

The net is conical, 100 cm diameter at the mouth, and 10 cm diameter at the cod

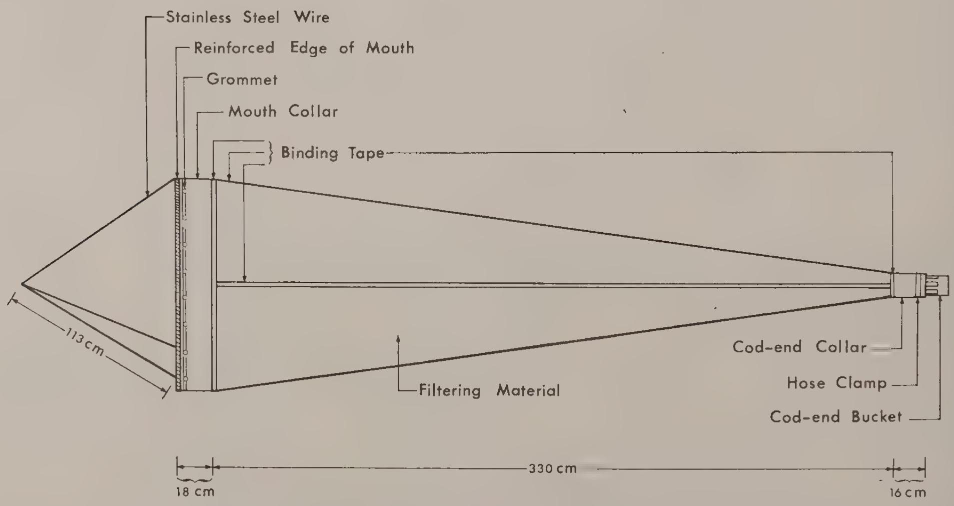
Stainless Steel Wire
Reinforced Edge of Mouth
Grommet
Mouth Collar
Binding Tape
113 cm
Filtering Material
Cod-end Collar
Hose Clamp
Cod-end Bucket
18 cm
330 cm
16 cm

FIG. 1. Principal components and dimensions of the ICITA one-meter plankton net.

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[1] Contribution No. 33, Tropical Atlantic Biological Laboratory, Bureau of Commercial Fisheries, Miami, Florida.

[2] 167 Palmer Avenue, Falmouth, Massachusetts 02540.

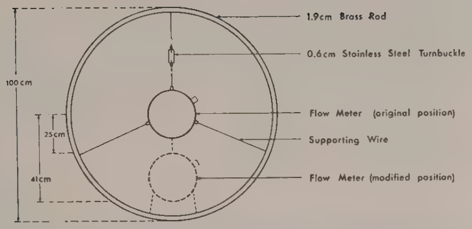
1.9cm Brass Rod
0.6cm Stainless Steel Turnbuckle
100 cm
Flow Meter (original position)
25cm
Supporting Wire
41cm
Flow Meter (modified position)

FIG. 2. Diagram of flowmeter attachment to mouth ring of the ICITA net.

end (Fig. 1). The nonfiltering portion of the net consists of the mouth and cod-end collars made of No. 10 canvas. The forward edge of the mouth collar is sewed around a ⅜-inch (0.9 cm) diameter three-strand manila line running along the circumference of the mouth; 26 No. 2 brass grommets are used to lace the net to the towing ring. The grommets are positioned 3.5 cm behind the forward edge of the mouth.

The filtering portion of the net is composed of four regular trapezoidal panels of Nitex[3] No. 280, each with bases of 78.5 cm and 7.9 cm, and a height of 330 cm. These panels are sewed to each other and to the mouth and cod-end collars with ½-inch (1.3 cm) nylon banding tape; all seams are double-turned. The filtering material has mean aperture dimensions of 0.281 × 0.281 mm, a mean thread size of 0.171 mm, and contains an open area of 42%. Ratio of total area of netting apertures to area of net mouth is 3.09 : 1 excluding the nonfiltering portions of the net, such as the canvas collars and nylon seams.

Lacing, made of ¼-inch (0.6 cm) diameter braided nylon cord, attaches the mouth collar to the towing ring. The ring itself is made from round ¾-inch (1.9 cm) brass stock. The bridle consists of three stainless steel wires, which lead from the towing ring to a galvanized swivel forward of the center of the mouth opening. A line 2 m long leads from the swivel to the towing warp.

A flowmeter is held in place in the center of the mouth opening by three stainless steel wires, one of which is fitted with a turnbuckle (Fig. 2).

The cod-end bucket, which is attached to the net by a hose clamp, consists of three parts (Fig. 3): 1) a polyvinyl chloride bucket with five draining slots; 2) a sock made of No. 280 Nitex, which fits inside the bucket; and 3) a flanged, circular insert which extends into the bucket to secure the sock during towing.

Following a tow, the sample is rinsed into the cod-end sock. The bucket is then detached from the net, the insert removed, and the sock with the sample lifted out. The sample can be transferred to a specimen jar by inserting the open end of the sock and rinsing its contents into the jar, using a rinse bottle containing seawater or 5% formalin.

Flume experiments on the ICITA net showed that filtering efficiencies (100 × water accepted/water encountered) were higher than 95% at towing speeds of 51–257

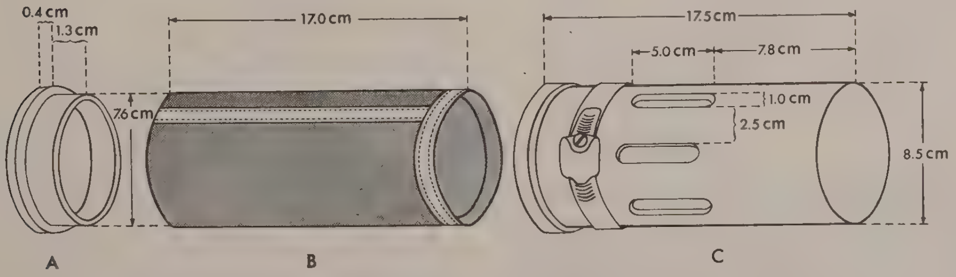

FIG. 3. Exploded diagram of cod-end bucket of the ICITA net.

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[3] Tobler, Ernst & Traber, Inc., 71 Murray Street, New York, N.Y. 10007.

cm/sec (Mahnken and Jossi, in press). These sustained high filtering efficiencies may have resulted, in part, from stretching of the nylon mesh material. Clogging did not lower the efficiencies (as it might have done under less controlled conditions), because the flume tests were conducted in "clean" water.

The flume tests also revealed the presence of a core of low-velocity water behind the towing bridle. To obtain a more accurate measure of the volume of water entering the net, the flowmeter was moved from its central location to a point 25 to 40 cm from the center of the net (Fig. 2), where the flow better represented the average for the entire mouth.

The compactness of the ICITA net makes it especially suitable for use at sea. It can be rinsed thoroughly by a gentle spray from the outside, while it hangs vertically over the deck. Because of its convenience and manageability, the net also can be used by small research vessels.

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THE DETERMINATION OF MANGANESE AND IRON IN SEA WATER BY ATOMIC ABSORPTION SPECTROMETRY

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ABSTRACT

Coprecipitation and solvent extraction techniques were investigated as means of concentrating manganese and iron from sea water for atomic absorption analysis. Quantitative recovery was achieved with 20X concentration by a single-step extraction with sodium diethyl dithiocarbamate into methyl isobutyl ketone. The low levels of these metals in ocean waters indicate that greater concentration factors are needed to achieve better precision, which is limited by readout error.

RESUME

Des recherches ont été faites sur des méthodes de précipitation simultanée et d'extraction de solvants en tant que moyens de concentration du manganèse et du fer de l'eau de mer à des fins d'analyse par absorption atomique. On a recupéré un concentré accru d'un facteur de 20 par extraction unique au diethyldithiocarbamate de sodium dans de l'isobutylmethylcetone. Les faibles teneurs des eaux de mer en ces métaux exigent de plus forts accroissements de la concentration si l'on veut obtenir une précision meilleure qui est d'ailleurs limitée par les erreurs de lecture.

ZUSAMMENFASSUNG

Verschiedene chemische Methoden der Probenanreicherung für Mangan und Eisen in Ozeanwasser wurden untersucht, um A. A. Analyse zu ermöglichen. Quantitative Wiedergewinnung mit 20-facher Anreicherung durch einen Auszug mit NaDEDTC in Methylisobutylketon wurde erreicht. Die geringe Konzentration dieser Metalle in Ozeanwasser benötigt noch grössere Anreicherungen, um bessere Genauigkeit zu erzielen.

INTRODUCTION

The concentrations of many trace elements in sea water are known to vary widely, sometimes by several orders of magnitude (1). The data currently available have been obtained from relatively few samples and by a variety of methods which have not always yielded comparable results. The reliability of such data can be strengthened by the development of sensitive analytical techniques which can be standardized and applied readily to the processing of large numbers of samples.

Atomic absorption spectrometry, reviewed by Allan (2), has much to recommend it for the quantitative analysis of trace metals in sea water; it is sufficiently sensitive for the analysis of many metals in concentrations in the range of parts per billion to parts per million, and it is relatively free from spectral interferences. Fabricand et al. (3) were the first to employ atomic absorption for the analysis of sea water. The total concentrations of copper, zinc, iron, manganese, and nickel were determined directly in untreated samples. Better precision for determinations at the low levels at which these elements occur in sea water may be achieved either by preconcentration of the sample as suggested by Burrell (4) or by modification of the instrumentation to increase the absorption path.

Because of their biological significance and erratic distribution in sea water, iron and manganese are of particular interest to oceanographers, but their precise determination has presented formidable difficulties, which atomic absorption analysis should be able to reduce. In sea water, these two elements are distributed among the particulate, colloidal, and dissolved phases (5). The particulate and colloidal phases may be concentrated by retention on membrane filters (now available with pore sizes of 0.1 μ diameter and less) which may then be prepared for atomic absorption analysis by ashing and taking up the residue in acid aqueous solution. In the dissolved phase, manganese and iron have been reported to occur as ionic species and as components of organo-metallic complexes (6). We have been investigating the preconcentration of the dissolved fraction of these and other trace elements in sea water in preparation for atomic absorption analysis, and in this report will present some of our experiences with coprecipitation and solvent-extraction techniques.

INSTRUMENTATION

A Perkin-Elmer Model 303 atomic absorption spectrometer and an automatic null recorder readout accessory were used with a Photovolt Linear/Log Varicord Model 43 strip-chart recorder. Instrumental conditions were as shown in Table I.

TABLE I
Analytical Conditions

	Manganese	*Iron*
Source	Hollow cathode	Hollow cathode
Wavelength	2795 A	2483 A
Slit	3.0 mm (bandpass 20 A)	0.3 mm (bandpass 2 A)
Flame	Stoichiometric air-acetylene	Stoichiometric air-acetylene
Scale Expansion	10X	10X
Noise Suppression	Setting 3	Setting 4

SEA-WATER SAMPLES

The sea water used in these investigations was selected at random from samples collected at depths from 0 to 100 meters in an area from 10 to 100 miles offshore between the northern end of Vancouver Island and the mouth of the Columbia River. The samples were collected in 6-liter Van Dorn-type bottles made of polyvinyl chloride, filtered through HA (0.45 μ) millipore filters, and stored frozen in polyethylene bottles.

SINGLE-STAGE CONCENTRATION: COPRECIPITATION

Additions of manganese (as $MnSO_4$) from 0.5 to 2.0 μg were made to 200-ml subsamples of the same sea-water sample in stoppered 250-ml polyethylene graduated cylinders. Following the procedure of Koroleff (7), 10.0 ml of 0.2N KOH were added to each cylinder, which was then thoroughly shaken and left standing overnight to allow the precipitate to settle. All but about 25 ml of the supernatant liquid was siphoned off, and the precipitate was redissolved by the addition of 5.0 ml of 0.25N HCl.

The redissolved precipitate from one sample was aspirated directly into the flame of the spectrometer. Absorption readings were erratic (possibly because of scattering of the beam by unvolatilized particles in the flame), and for this reason it was decided to separate the heavy metals from the carrier before analysis.

TWO-STAGE CONCENTRATION: COPRECIPITATION — SOLVENT EXTRACTION

The ability of dithiocarbamates to form transition-metal chelates which are readily extractable into organic solvents is well known. Most of the heavy metals will chelate with ammonium pyrrolidine dithiocarbamate at a pH as low as 2.5 (8). Sodium diethyl dithiocarbamate (DEDTC) is considerably cheaper, however, and at pH 6-9 is satisfactory for the formation of extractable complexes with manganese and both ferrous and ferric iron (9).

The redissolved precipitates from the remaining samples were transferred to Babcock cream-test bottles (10) and 2.0 ml of a 5% solution of sodium DEDTC were added to each. After not less than 15 minutes, 5.0 ml of MIBK were added and the phases mixed by shaking for two minutes. The bottles were then centrifuged to accelerate separation of the phases. This is important, as the manganese chelate is unstable in MIBK (11) and slowly precipitates. Determinations should take place within one-half hour of extraction. After separation of the phases, deionized water was added to bring the organic phase into the neck of the bottle for convenient aspiration into the atomic absorption flame. A plot of absorbance against the additions of manganese is shown in Figure 1. The instrument was zeroed on reagent-grade MIBK. The linearity of the plot indicates quantitative recovery of the manganese. A similar procedure was followed using a new set of samples with additions of iron as ferrous ammonium sulfate. The results are shown in Figure 2. The linearity of the plot again indicates quantitative recovery.

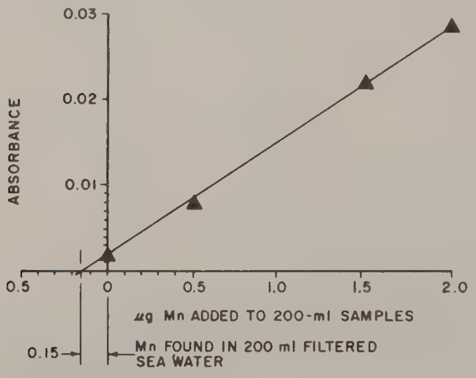

Fig. 1 — Atomic absorption of manganese in DEDTC extracts after coprecipitation from sea water.

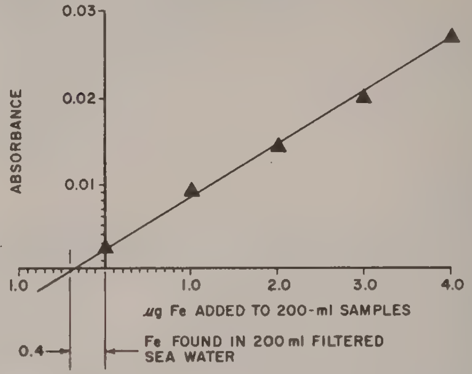

Fig. 2 — Atomic absorption of iron in DEDTC extracts after coprecipitation from sea water.

SINGLE-STAGE CONCENTRATION: SOLVENT EXTRACTION

Further tests were made to determine whether the concentration procedure could be simplified by eliminating the coprecipitation step and extracting the manganese and iron directly from the sea-water samples. In these tests, 10.0 ml of 5% sodium DEDTC were added to 200-ml samples of sea water in 250-ml separatory funnels containing additions of manganese and iron standards. After 15 minutes, 10.0 ml of MIBK were added, and the mixtures thoroughly shaken for two minutes. After 20 minutes, the organic phase and that part of the aqueous phase containing the remaining organic suspension were transferred to Babcock bottles. The separatory funnels were rinsed with a small amount of deionized water, and the rinsings were drained

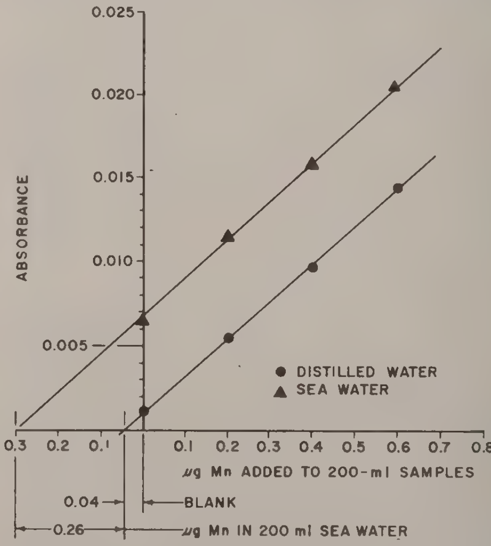

Fig. 3 — Atomic absorption of manganese extracted directly with DEDTC.

into the Babcock bottles, which were then centrifuged to complete the phase separation. Deionized water was added to bring the organic phase into the necks of the bottles for convenient atomic absorption analysis. In addition, for the purpose of blank determination, the procedures were repeated with additions of manganese and iron to distilled water. In each case the instrument was zeroed on reagent-grade MIBK. The results, shown in Figures 3 and 4, include corrections for the difference in volume of MIBK recovered from sea-water and distilled-water samples.

Tables II and III show the results of tests for interferences in the atomic absorption analyses of manganese and iron from zinc and copper, as well as from each other. Zinc and copper are also extracted by DEDTC-MIBK, and occur in sea water at levels comparable to, or in excess of, those of manganese and iron.

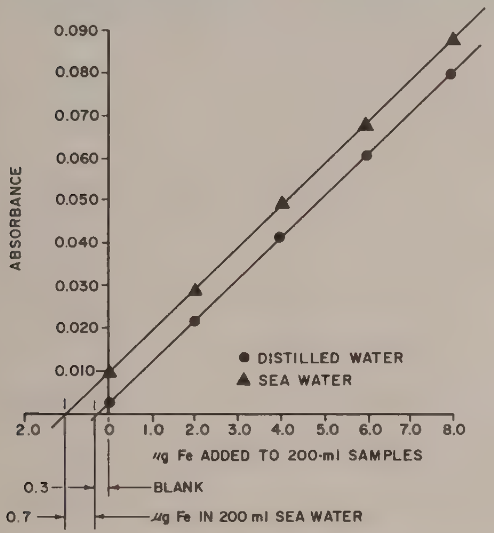

Fig. 4 — Atomic absorption of iron extracted directly with DEDTC.

TABLE II

Tests for Iron, Zinc, and Copper Interferences in Manganese Determinations

Elements Added	µg Added to 200 ml Sea Water	Absorbance
Mn	1	0.0132
Mn, Fe	1, 5	0.0132
Mn, Zn	1, 5	0.0128
Mn, Cu	1, 5	0.0132

TABLE III

Tests for Manganese, Zinc, and Copper Interferences in Iron Determinations

Elements Added	µg Added to 200 ml Sea Water	Absorbance
Fe	2	0.0123
Fe, Mn	2, 5	0.0123
Fe, Zn	2, 5	0.0123
Fe, Cu	2, 5	0.0123

REPRODUCIBILITY

The results of six analyses for manganese and iron in 200-ml subsamples of the same sample of sea water are shown in Table IV. Since the interval between the smallest scale divisions on the chart paper used in the recorder represented 0.0004 absorbance unit, it is apparent that at these low absorbance values, readout error alone would be in the range between 10 and 20%. In another test of reproducibility, a large sample of 0.017 ppm manganese as the DEDTC complex in MIBK was repeatedly analyzed to determine whether instrumental variation would be a significant factor at such low absorbance values.

TABLE IV

Replicate Determinations of Manganese and Iron Extracted from Sea Water

Sample Number	Absorbance	
	Manganese	Iron
1	0.0026	0.0022
2	0.0026	0.0022
3	0.0026	0.0026
4	0.0026	0.0022
5	0.0026	0.0022
6	0.0031	0.0026

The results are shown in Table V. The observed variation did not exceed that to be expected from readout error.

TABLE V

Replicate Analyses of an MIBK Solution of 0.017 ppm Manganese as the DEDTC Chelate

Sample Number	Absorbance	Sample Number	Absorbance
1	0.0015	6	0.0017
2	0.0017	7	0.0017
3	0.0017	8	0.0017
4	0.0015	9	0.0017
5	0.0017	10	0.0017
		11	0.0017

DISCUSSION

These experiments have demonstrated the feasibility of employing a single-step solvent extraction for the preconcentration of manganese and iron in the atomic absorption analysis of sea water for these elements. With a 20X concentration from 200-ml samples, quantitative recovery of these elements was possible. There are, however, several features of this technique which demand caution in its application to oceanographic analyses: 1) low absorbance values with respect to the magnitude of readout error limit the precision to a level which still leaves much to be desired; and 2) chelation at the natural pH of sea water does not guarantee the recovery of those portions of manganese and iron in true solution which are organically bound.

Since the volume of sea water available for analysis is limited chiefly by the size of the sampling device, and since precision is enhanced by optimum concentration of the element of interest in the solutions to be analyzed, we are currently devoting our attention to the problems of preconcentrating trace metals from much larger volumes of sea water. In preliminary experiments with radioactive tracers, better than 98% of the zinc in 1500 ml of sea water were recovered as the DEDTC chelate with a single 75X extraction with MIBK. At this extraction ratio, however, only 46% of manganese and 33% of iron were recovered. In another experiment, better than 98% of the cobalt in 20 liters of sea water was recovered as the DEDTC chelate on a 17-mm-diameter by 50-mm ion-exchange column containing Bio-Rad 1X8 resin of 100-200 mesh. All of the cobalt on the column was successfully transferred to an aqueous phase by slurrying the resin with three successive 10-ml portions of hot nitric acid. We are currently working on an adaptation of this technique for shipboard preconcentration of trace metals from sea water collected in 64-liter Bodman samplers.

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IMMOBILIZING, TRANQUILIZING, AND ANESTHETIZING DRUGS USED ON FUR SEALS (*Callorhinus ursinus*)

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Immobilization

The most extensive test of immobilizing drugs on the fur seal (*Callorhinus ursinus*) was carried out by Peterson (1965), who injected nearly 300 animals during the summers of 1961, 1962, and 1963 on St. Paul Island, Alaska. He tested the following drugs: phencyclidine, succinylcholine, thiopental sodium, propriopromazine, insulin, nicotine, and gallomine. Peterson usually administered drugs via projectile syringe into the latissimus dorsi muscle, posterior to the axilla. Best results were with phencyclidine and succinylcholine, but neither drug was entirely satisfactory. Phencyclidine required a long recovery period and the dosage of succinylcholine could not be standardized. Of 89 territorial bulls, 58 were immobilized, 13 never became affected enough for handling, and 18 died from overdosage.

Special considerations with regard to the use of immobilizing drugs were well covered by Harthoorn (1965). In immobilizing fur seals we are confronted with many of the same problems.

To achieve the best results we must have rapid absorption. Since intravenous administration by dart syringe would be purely accidental, we are forced to use the next best route, intramuscular. To obtain rapid absorption by the intramuscular route the drug must be concentrated and delivered into a muscle and not into subcutaneous fat. Physical exertion without fright speeds absorption and action of the drug.

In the fur seal the superficial or subcutaneous blubber is thin mid-dorsally and the thickness increases ventrally, becoming greatest around the elbow. A second or deep layer of blubber that lies beneath the cutaneous muscle is particularly thick over the latissimus dorsi muscle and over the thigh. A thinner layer covers the external abdominal oblique. The neck of a fur seal bull is one of the most muscular parts of his body. It is actually a weapon, since bulls fight by rapid extension of their necks to strike with their canines. A good target for a dart syringe, therefore, is the large muscular hump of the neck where the blubber layer is relatively thin.

Two additional points are important. The weight of an animal must be estimated with fair accuracy; this estimation requires practice. The drugs used must be highly soluble or compressible into a small volume.

Harthoorn (1965) successfully used a combination of phencyclidine, diethylthiambutene, and hyoscine for immobilization of large animals. His suggested dosage for a 1,000-pound animal is:

phencyclidine	(Sernylan)[1]	100 mg
diethylthiambutene	(Themalon)	1250 mg
hyoscine	(Scopolamine)	50 mg

A similar mixture was prepared for trial on the fur seals but with dihydromorphinone (Dilaudid) instead of Themalon. The latter has morphine-like action but fewer side effects (Owen, 1955). The former has five times the analgesic power of morphine and also fewer side effects (Jones, 1956). The trial dosage of this mixture was 1 cc per 100 pounds where 1 cc contained the following:

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[1] Trade names referred to in this publication do not imply endorsement of commercial products.

phencyclidine	(Sernylan)	10 mg
dihydromorphinone	(Dilaudid)	5.5 mg
hyoscine	(Scopolamine)	3.0 mg

An adult female fur seal, estimated to weigh 45 kg (100 pounds), was captured with a snare stick and injected in the gastrocnemius muscle with 1 cc of the above mixture. Seven minutes after the injection she was unable to stand or move away. After 13 minutes she could be handled easily, and after 20 minutes was insensitive to ordinary external stimuli. There were no signs of excessive respiratory depression. She recovered sufficiently in 2-1/2 hours to remingle with the herd (Keyes, 1966).

A healthy appearing young bull, estimated to weigh 160 kg (350 pounds), was given 3.5 cc of the same mixture injected into the dorsal hump of the neck by a dart syringe. The bull gradually slumped down on his sternum 7-10 minutes after the injection. He did not flinch after 25 minutes when the barb was surgically removed. Anesthesia was still fairly deep after 45 minutes but he responded to a pull on a vibrissa by nodding his head slightly. After 3 hours the bull was sleeping heavily but stood up when prodded. He gave no signs of excessive respiratory depression. The next morning he was completely recovered except for photophobia (Keyes, 1966) caused by the hyoscine (Harthoorn, 1965).

A second female, weighing 35 kg (77 pounds), was immobilized with 0.8 cc of the mixture to obtain a milk sample and was kept in a cage during recovery. Induction was similar to that in the first female. Recovery was somewhat stormy, probably owing to the stimulus of loud noises made by workmen nearby. The female appeared normal when released the next morning (Keyes, 1966).

This drug mixture has the advantages of rapid intramuscular absorption and rapid induction to a useful plane of anesthesia for a convenient period of time. The margin of safety appears to be wide and the volumes of anesthetizing doses are small. The disadvantages are the long recovery period and prolonged dilation of the pupils and its interference with visual accommodation (Harthoorn, 1965).

Tranquilization

Propriopromazine (Tranvet) was injected intramuscularly in two female fur seals at the rate of 0.55 mg per kg (0.25 mg per pound). This dosage had little effect on their belligerence but I believe they were not as strong as they otherwise might have been (Keyes, 1963).

A higher dosage of 4.4 mg per kg (2 mg per pound) produced sedation deep enough for a lactating female to be strapped to a milking platform (Keyes, 1963). Some females are more belligerent than others and require more drug. One such female received one injection of 300 mg followed in 30 minutes by 100 mg and 30 minutes later by another 100 mg, for a total of 500 mg within an hour (Keyes, 1964). This dosage of 11.1 mg per kg (5 mg per pound) is 100 times the tranquilizing dose for a horse. Even at this high dosage she still tried to bite. Better sedation was achieved in another female with 400 mg (8.8 mg per kg or 4 mg per pound) injected in a single dose (Keyes, 1966).

Tranvet at a dosage of 4.4 mg per kg (2 mg per pound) of body weight rendered a male fur seal of approximately 45 kg (100 pounds) tranquil enough for intravenous injection of an anesthetic (Keyes, 1963).

The general attitude of tranquilized seals is one of somnolence, although they can still be stimulated to bare their teeth. The main advantage is in overcoming their strength and agility. Tranvet takes effect in 15 to 60 minutes. At high dosage the deep sedation wears off in 3 to 5 hours but some degree of calming lasts from 12 to 24 hours.

Anesthetization

A 45 kg, 4-year-old male fur seal was anesthetized with thiamylal sodium (Surital). One hour after the intramuscular injection of Tranvet as a preanesthetic, the seal's foreflipper was drawn through a slot in the side of the cage to permit injection of the anesthetic into the cephalic vein where it crosses the volar surface of the carpus near the junction of fur and flipper skin. Five cc of 4 percent Surital were injected steadily in a period of about 10 seconds. Surgical anesthesia, to near abolishment of the palpebral reflex, was reached quickly and smoothly. Pulse and breathing rates were strong and regular. After about 15 minutes, during cannulation of the carotid artery and external jugular vein, the seal began reacting to pain of surgery and was carried back down to the desired plane of anesthesia with 2 additional cc of Surital. A third injection of 1 cc, making a total of 8 cc, was necessary to complete the cannulations (Keyes, 1963). The potentiating effect of the tranquilizer Tranvet was marked. On the basis of data for dogs, the calculated dose of 4 percent Surital to achieve surgical anesthesia was 20 cc (1 cc per 5 pounds of body weight or 3.8 mg per kg (Jones, 1956)) but only 5 cc was needed.

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BUREAU OF COMMERCIAL FISHERIES INTERESTS IN ESTUARINE ECOLOGY

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For well over half a century the Federal Government has been conducting research on estuarine and marine organisms of economic importance at its biological laboratory in Beaufort, North Carolina. This laboratory, founded in 1899 and now administered by the Bureau of Commercial Fisheries within the Department of the Interior, is located on Pivers Island which lies less than 2 miles inside Beaufort Inlet and about 150 yards from the town of Beaufort proper. Early work by laboratory personnel included studies on the distribution, general life history, and habits of such diverse creatures as various finfishes, sponges, shipworms, the oyster, bay scallop, and diamondback terrapin. In marked contrast, almost all present-day research centers on a single group of fishes, the commercially valuable menhadens that occur abundantly off both the Atlantic and Gulf coasts. The only other fish or shellfish on which the laboratory is doing research are the blue crab and American shad. It is generally recognized that the estuary plays an important role in the life cycle of each of these three forms.

Because the laboratory has been assigned the task of carrying out all federally sponsored research on the Nation's menhaden resources, its scope of responsibility, geographically speaking, is accordingly as broad as the combined ranges of the various menhaden species and their fisheries. As a consequence, laboratory personnel are seasonally deployed far beyond the boundaries of North Carolina, in fact all the way from New England on the north to the Texas-Louisiana border on the south. Likewise, the laboratory is charged with conducting all Bureau research on Atlantic coast shad, although present work is restricted to several rivers that provide spawning areas for this anadromous species. Investigation of the blue crab, on the other hand, is largely confined to North Carolina waters.

The general mission of Bureau research at the Beaufort laboratory is to develop much-needed information about the biology and dynamics of the commercially important species just mentioned. Our ultimate goal is the formulation of guidelines for managing these resources so that each will always yield the maximum harvest allowable under prevailing environmental conditions. Pursuit of this worthy goal automatically involves us in all the disciplines encompassed by the term fishery biology, not the least of which is the ecology of each species being studied. At the moment our activity in the field of ecology is somewhat limited by insufficient funds and manpower, but anticipated increases in the laboratory's budget could quickly change this situation.

Research findings by laboratory personnel are disseminated through publication in scientific journals, presentations before various industry groups, and communications to the Atlantic and Gulf States Marine Fisheries Commissions. Both Commissions are the result of congressional action, in which the Bureau of Commercial Fisheries is identified as their principal arm of research.

MANPOWER AND FACILITIES

The Beaufort biological laboratory houses a professional staff of 22 fishery biologists, more than half of whom are engaged in research on menhaden. Of this total 18 hold advanced degrees. Permanent support personnel number 20.

Research facilities include a continuous-flow saltwater system that supplies a dozen or more indoor and outdoor aquaria ranging in capacity from a few gallons to over 1,200; several small ponds for holding populations of experimental fish; six 50-cu.-ft. cabinets and two 370-cu.-ft. rooms in which the temperature of simulated environments can be precisely controlled; and a fairly comprehensive library in fishery science and related fields. In addition, a fleet of small inboard and outboard craft and four trawling vessels that range in length from 26 to 45 ft. give the staff a high degree of mobility in gathering biological, physical, and chemical data from estuarine waters harboring the various species of interest.

If anticipated increases in the laboratory's budget materialize, plans are to acquire a suitable vessel for offshore work in the Atlantic Ocean and Gulf of Mexico, to develop a more versatile facility for studying fish physiology and behavior, and to increase the amount of office and work space now available.

Other groups doing related research in the Beaufort area, with whom the laboratory staff has frequent contact and occasionally shares facilities, are the Bureau's Radiobiological Laboratory and Duke University's Marine Laboratory on Pivers Island, and the University of North Carolina's Institute of Fisheries Research in Morehead City.

CURRENT RESEARCH PROGRAMS

As stated earlier, research at the Beaufort biological laboratory is directed mainly toward three marine resources, each of which is estuary-dependent at some stage in its life history. Moreover, these resources support commercial fisheries that rank among the most important not only in North Carolina but in nearly all other Atlantic and Gulf coast states as well. Within the laboratory's overall operation, the three resources--menhaden, blue crab, and shad (anadromous fish)-- are identified by their own programs whose features are briefly described below. Since these programs are species oriented by definition, it follows that current or proposed ecological studies are or will be largely structured along the same lines. Significant departures from the present "species" approach appear unlikely in the immediate future, although an opinion being expressed with increasing frequency at higher organizational levels is that Bureau commitments in marine and estuarine research, much of which is of an ecological nature, might be considerably more meaningful if approached from the "ecosystem" point of view.

Menhaden

Of all the Nation's commercial fishery resources, the Atlantic and Gulf menhadens annually yield the greatest tonnage. In 1965, menhaden landings totaled slightly more than 1.6 billion pounds, or about 40 percent by volume of the total U. S. Catch of all species. A disturbing note, however, is that the yield of Atlantic menhaden in 1965 (just above 600 millio pounds) represented yet another point on a sharply downward catch trend that began in 1963 following high production the year before. Significantly, the 1965 catch was 47 percent below that landed in 1962 and 61 percent less than the record catch of 1956. Because of the acute situation in the Atlantic menhaden fishery, both industry and government spokesmen are more aware than ever before of the need for an expanded program of federal research that would provide guidelines for restoring and thence maintaining the high productivity of this important resource.

For those unfamiliar with the species, menhaden are fairly small herringlike fishes that are reduced for industrial use to meal, oil, and solubles. They have an interesting life cycle in which myriads of eggs are spawned and hatch at sea; the larvae (at an age of about 6 weeks) move into estuaries where they soon transform into juveniles; the juveniles enter the lower reaches of tributary streams where they grow for 6 or more months to subadulthood; and the subadults eventually emigrate to the sea where they mature and thus complete the cycle. Menhaden are schooling fish and, although a few are caught in pound nets erected near the mouths of bays and sounds, most are taken with purse seines (at an age of 1 year or more) in the ocean and larger bays.

The Menhaden Program is divided into projects that treat by scientific discipline and in varying depth all stages of menhaden life history. Under the heading of general biology, work is underway to determine when, where, and how intensely the major species spawn; what morphological characters distinguish the various species at their larval stages of development; whether and to what extent species with overlapping ranges interbreed; if populations of the two major species are truly homogeneous; and how rapidly the juveniles grow during their stay in the estuary.

In the realm of ecology, studies are in progress to ascertain under laboratory conditions the young menhadens' limits of tolerance to such environmental factors as temperature and salinity. Field work in ecology is restricted at present to the development of techniques for estimating the density of juveniles in their estuarine habitat. Although a major goal of this work is to provide reliable time-series of menhaden abundance indices with which corresponding series of environmental variables can be correlated to establish ecological cause-effect relationships, the resulting measurements have also been and will continue to be used in assesing annual recruitment (or year-class strength) and in forecasting relative yields.

By far the greater share of attention in the Menhaden Program is being given to the study of population dynamics. In fiscal year 1966, for example, this activity consumed about two-thirds of all program manpower and funds. Two approaches characterize this phase of the program's total research effort: (1) systematic collection and analysis of fishery and biometrical statistics, and (2) execution of mark-recapture experiments. In the former, strategically located personnel regularly canvass reduction plants for information on menhaden production as well as fishing intensity. They also sample landings for data on population structure in terms of age, size, and sex. In the latter approach, menhaden into whose body cavity has been inserted a small, numbered, ferromagnetic tag are released in different areas throughout the range of the fishery being studied. For extended periods of time after release the marked fish are recaptured by the fishing fleets and returned to the reduction plants where, depending on the type of tag-recovery equipment in use, either the tags alone or the fish containing them are recovered. Analyses of the resulting data will provide needed measures of population growth and mortality. When properly synthesized, such measures will show to what degree the menhaden resources are being affected by fishing, and at what age each new generation of menhaden should begin to be harvested so that it will yield the maximum poundage during its life span. The mark-recapture work is also expected to give some indication of population movements.

Blue Crab

This popular shellfish supports the fastest growing commercial fishery in North Carolina and nationally ranks among the top six of our most important seafood resources. Crab landings in North Carolina during 1965 amounted to 22.7 million pounds, about a 20-percent increase over production in 1963 and 50 percent more than in 1960. The crab's life cycle resembles the menhadens' in that the eggs hatch at sea and the newly hatched individuals move or are transported by currents into estuaries. The young crabs gradually spread throughout the brackish environment into nearly fresh water, all the while growing very rapidly. With the onset of maturity they mate and the berried females eventually emigrate to the nearshore waters of the ocean where the eggs hatch and the cycle begins anew.

Practically all the research being performed by the Blue Crab Program falls into two categories: ecology and population dynamics. Ecological research has been chiefly confined to the laboratory and performed under contract by the Marine Laboratory of Duke University. Most of this work has dealt with the influence of changes in simulated environmental variables such as temperature, salinity, oxygen tension, and quality of food supply on the survival and rate of development of very young crabs. The program's population studies are focusing attention on the matter of crab growth during prefishable stages of development and, with the aim of developing a means of forecasting crab supplies, on the relationship between the density of juvenile crabs and the subsequent abundance of marketable adults.

Anadromous Fish

Although identified in such a way that one might get the impression it houses biological research on a variety of species, this program is concerned principally with just one, the American shad. Until very recently the laboratory was charged with the additional responsibility of conducting research on the striped bass. But when the objectives of the Bureau's original shad and striped bass programs were attained, the present activity was implemented to assist other Federal agencies and the Atlantic coast states in solving biological problems encountered during attempts to restore spawning runs of anadromous fishes above stream barriers, and in protecting such species from adverse changes in stream environment. Since the shad is the most important of these species, it has received more attention.

Like the blue crab, the shad has grown steadily in significance. It now supports thriving commercial fisheries in most east coast rivers and bays from northern Florida to Connecticut, as well as major recreational fisheries in the Connecticut, Delaware, Pamlico-Tar, Cape Fear, Edisto, Ogeechee, and St. Johns Rivers. In 1965 commercial landings alone exceeded an estimated 11 million pounds, up roughly 10 percent from production the year before.

As denoted by the term "anadromous," shad pass through a life cycle in which the parent fish, with the approach of the reproductive season in early springs, ascend coastal streams to fresh water where spawning and hatching take place. The young fish remain in the streams for 6 or 7 months and then move downstream and out to sea. Those that survive to maturity will eventually return to fluvial spawning grounds, perhaps on more than one occasion, and thus complete the life cycle.

With the large-scale development of coastal water resources, concern about the future of this and similarly adapted species is mounting rapidly. So the Bureau, through the Beaufort laboratory's Anadromous Fish Program, is working closely with state and other Federal agencies to offset the potentially harmful effects of stream-control structures and streamside industrialization. At present, practically all program research is devoted to the general problem of passing gravid shad over dams and through navigation locks located on several of the aforementioned rivers. Complementary work on one, the Susquehanna River, should establish the suitability of that river's upstream environment and hence the feasibility of restoring runs of spawning shad above certain dams, i.e., in areas excluded to the species since the dams were erected many years ago.

Other Bureau Interests in Estuarine Resources

From the foregoing account, one should have no trouble developing an appreciation for the idea that estuaries are a vital element in the survival strategy of these and many other tidewater resources enjoyed by society. The Bureau and related Federal agencies share this concept and together play a significant role in lessening the harmful impact on estuarine resources of otherwise beneficial reclamation projects.

To help discharge Bureau obligations on matters relating to the protection of coastal wetlands, technical personnel at the Beaufort and other Bureau laboratories routinely define, upon official request, the probable adverse effects of water-development projects that threaten fishery resources like the menhaden, crab, and shad, and recommend ways in which such effects can be mitigated. At higher echelons, the Bureau also administers research in fishery biology and estuarine ecology conducted by the states and financed under Public Law 88-309, the Commercial Fisheries Research and Development Act. Work funded by this act and now underway in North Carolina is concerned with the well-being of the State's oyster and shrimp resources, both of which are estuary-dependent, and with changes in the general quality of the estuarine environment as a habitat for these and a host of other brackish-water forms. The details of this work are reviewed elsewhere in the Symposium.

PROSPECTIVE ACTIVITIES

Though seemingly broad in scope, the Beaufort laboratory's research program is in many respects somewhat superficial. This situation becomes readily understandable when one considers the extensive distribution of the fishery resources whose study as a Bureau responsibility has been assigned to this laboratory, the wide range of environmental conditions under which they exist, and the numerous as well as varied problems that are met in their conservation. Compounding the logistical difficulties posed by the resources themselves has been a traditionally modest allotment of manpower and operating funds. Still awaiting answers nevertheless are such important questions as: What causes year-to-year fluctuations in the supplies of these resources? Have any of them been overfished? and, In the face of an ever-changing aquatic environment, how should their exploitation be regulated so that they yield maximum sustainable harvests?

To answer these questions we envision a significantly larger research budget than is now appropriated. Some relief appears to be in sight as of this writing, principally to support an expanded program of research on menhaden, the east coast fishery resource now experiencing the most serious difficulty. In addition to bolstering certain portions of the Bureau's present menhaden investigation, supplemental funds will be used (1) to begin a study of ecological factors affecting the survival and development of young menhaden during their oceanic phase, and (2) to increase research in the field of experimental ecology. From the latter work Bureau scientists hope to acquire more definitive information on the physiological and behavioral response of embryonic, larval, and juvenile menhaden to changes in the physicochemical properties of their environment.

Some expansion also appears likely in the Anadromous Fish Program. Extra money and manpower are possible if this program is to share the task of administering the biological research on anadromous species to be performed by east coast states under the provisions of Public Law 89-304, the Anadromous Fish Act.

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The Role of Estuaries in the Development and Perpetuation of Commercial Shrimp Resources

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The Role of Estuaries in the Development and Perpetuation of Commercial Shrimp Resources

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ABSTRACT

This report summarizes knowledge concerning functional relationships between the estuarine environment and commercial shrimp resources. Discussion is largely restricted to North American species; attention is focused upon situations evolving specifically as a result of the rapid urban and industrial development of our estuary-rich Gulf coast.

The association of shrimp and the brackish-water environment from ontogenetic and ecological points of view is reviewed. The question of continued productivity and perpetuation of shrimp stocks in the face of man's steady incursion of estuaries is considered. Also considered are measures that might be taken to counteract real, or imagined, effects of society's development of coastal wetlands.

INTRODUCTION

The broad, potential significance of the Nation's coastal swamplands, or "wastelands," as many have called them, was not recognized until fairly recently. Perhaps their first bounty, going back to the days of the early settlers, was realized in the form of furbearers, waterfowl, and fish—most of which still flourish in many of these areas. But it soon became apparent (Davis, 1956) that our vast estuaries offered much more: wetlands that could be rather easily "reclaimed" and then farmed, urbanized, or industrialized by an expanding society; ready-made cesspools for our manifold wastes; waters that could be deepened for waterborne transportation; underlying mineral deposits to extract; natural areas to develop for conflicting recreational uses; and freshwater inflow for diversion to municipal, industrial, and agricultural needs in regions of low rainfall. Such activities pose an ever-increasing threat to those creatures which collectively represent what should be viewed as a natural heritage to be carefully husbanded for food and fun in future generations.

It is unfortunate that in most instances we can only speculate about the possible demise of fishery resources seemingly dependent upon or inseparably linked to the estuary. Not the least of such resources are the stocks of shrimp of which our society is making relatively great demands, and upon which it consequently places a high economic value. Just what is their relation to the estuarine environment? And, with man's steady incursion of our estuaries, what does the future hold for their perpetuation and continued productivity? Finally, what measures can be taken to offset the untoward effects of a rapidly progressing civilization?

At this point, it might be well to explain what is meant by the term "estuary." Webster's dictionary merely defines it as: "A passage where the tide (of the sea) meets the river current; especially, an arm of the sea at the lower end of a river . . ." In practice, as Ketchum (1953) points out, such a general definition does not sufficiently describe all estuaries. They range in diversity of configuration and character from the simple Scandinavian fjord to the extensive deltaic complexes at the mouths of large rivers like the Ganges, Amazon, and Mississippi. In between one can note the labyrinthine marshes that characterize the Chesapeake Bay area and lowlands of eastern New Jersey; the broad flats at the mouths of the Thames and the Elbe River in western Europe; the geologically interesting confines of San Francisco Bay; and the shallow-gradient Gulf coast of Texas and Louisiana that is a confusion of bays, rivers, creeks, bayous, and marsh.

To clarify, an estuary is neither the saltwater environment of the open sea, nor the freshwater environment of the river. It is a dynamic part of each, both the edge of the sea and the edge of the land; a buffer zone that is in a continual state of flux, being af-

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TABLE 1.—*United States imports of shrimp from various countries over the period 1950–64. Viewed serially, the data are intended to serve as rough indices of the degree to which shrimp fisheries are developing in different parts of the world*

[Millions of pounds, headless[1]]

Country of origin	1950	1956	1960	1961	1962	1963	1964
British Guiana	–	–	3.6	3.5	4.1	5.5	5.5
Ecuador	–	3.0	4.2	4.7	5.1	5.6	5.8
El Salvador	–	–	6.7	8.1	7.2	6.7	6.3
India	–	1.0	2.9	3.2	5.6	9.9	10.2
Japan	0.1	2.6	2.9	1.8	3.9	4.1	2.9
Korea (South)	–	–	–	0.2	1.8	2.2	1.3
Mexico	39.7	53.7	73.6	79.2	77.7	76.5	72.1
Pakistan	–	–	1.0	1.7	3.2	3.7	4.8
Panama	0.1	5.8	8.4	9.9	10.1	10.3	12.1
Unspecified	0.3	2.5	10.1	14.0	22.5	27.0	33.6
Total imports	40.2	68.6	113.4	126.3	141.2	151.5	154.6
United States production	114.0	133.4	148.5	103.9	119.2	150.7	131.1
Ratio of imports to domestic production	1:2.8	1:1.9	1:1.3	1:0.8	1:0.8	1:1.0	1:0.8

[1] Import figures for 1960–64 are conservative since they include moderate quantities of fully processed shrimp (i.e., shrimp without heads as well as those cooked and with the "shell" removed), which were not converted to units of headless weight.

Source: Fisheries of the United States, 1961, 1962, 1963, and 1964. C.F.S. Nos. 2900, 3200, 3500, and 3800. Bureau of Commercial Fisheries, U. S. Fish and Wildlife Service.

fected in varying degree by the sea, by the land, by the season, even by the hour of the day—as the ecologist would say, "an ecotone" in the truest sense of the word. From the above, the reader should encounter no difficulty visualizing throughout this report what is meant whenever the term "estuary" is employed.

To the continually changing environment so described there has become adapted an assemblage of many floral and faunal types. And within each estuary—simple or complex—there has developed accordingly a distinctive "ecosystem" composed of communities of biological elements exhibiting differential gradients of tolerance to each other as well as to an infinity of combinations of the physical and chemical factors that characterize it. From this ecosystem but a single constituent—the shrimp—has been selected for detailed discussion. The reader should strive at all times in the subsequent discourse to maintain in his thinking a contextural relationship between the shrimp and its associated fauna, particularly the fishes, molluscs, and other crustaceans.

IMPORTANCE OF THE NATION'S SHRIMP RESOURCES

Published fishery statistics quickly dispel any doubt as to the growing significance of shrimp in world trade (Table 1). Although these delicate crustaceans are viewed in most quarters as strictly a luxury food item, exploitation of shrimp stocks has played (and still plays) no small role in furthering the national economies of countries the world over. Beginning well before the turn of the century, but not making appreciable strides until after World War II, development of the world's shrimp resources continues at an ever-increasing pace. So strong has the demand for shrimp products become that not only is utilization of hitherto unfished stocks being accelerated, but serious efforts are underway in many corners of the globe to increase shrimp supplies through artificial means.

Statistics also disclose that the United States ranks first in volume of shrimp landings (Table 2). The relative importance of domestic shrimp resources can be readily gauged by noting that annual harvests fairly consistently yield a greater aggregate income at the production level than do those of any other fishery resource (Figure 1). In summary, the United States is the world's foremost producer as well as importer and consumer of shrimp, and internal shrimp fisheries together with all other segments of the shrimp industry occupy a relatively prominent position in the American economy.

The most important of United States shrimp resources are those that occur on the Continental Shelf and in estuaries at the edge of the Gulf of Mexico. Stocks lying off the Atlantic and Pacific coasts jointly contribute,

TABLE 2.—*Annual landings of shrimps and prawns during the period 1960–62 by the major shrimp-producing countries of the world*
[Millions of pounds]

Country	1960	1961	1962	Average	Rank
Brazil	51.6	57.5	–	54.6	6
Germany (West)	52.9	59.1	53.1	55.0	5
India[1]	155.6	142.9	185.6	161.4	2
Japan[1]	133.6	162.0	174.8	156.8	3
Mexico	147.3	159.4	155.6	154.1	4
Netherlands	28.4	29.8	30.9	29.7	8
Spain	36.4	32.0	30.2	32.9	7
United States	249.4	174.5	191.1	205.0	1

[1] Figures for these countries also include very small amounts of other crustaceans.

Source: Yearbook of Fishery Statistics, 1962. Volume XV, Food and Agriculture Organization of the United Nations.

TABLE 3.—*United States landings of shrimp by region in various years from 1956 to 1964*
[Millions of pounds, whole]

Coastal region	1956	1958	1960	1962	1964
North Atlantic	–	–	0.1	0.4	0.9
South Atlantic	25.6	22.6	31.2	26.1	17.4
Gulf of Mexico	193.6	173.3	205.7	141.7	179.0
Pacific	5.0	17.9	12.4	22.9	11.0
Total	224.2	213.8	249.4	191.1	208.3

Source: Fishery Statistics of the United States, 1956, 1958, 1960, and 1962. Statistical Digests Nos. 43, 49, 53, and 56; also: Fisheries of the United States, 1964. C.F.S. No. 3800, Bureau of Commercial Fisheries, U. S. Fish and Wildlife Service.

on the average, less than 20 percent to the total annual poundage of shrimp harvested by United States fishermen (Table 3). Year-to-year production in all areas is characterized by fluctuation of varying magnitude, explanations for which are currently being sought through State and Federal research programs.

During the first 4 years of the 1960's, commercial landings in Gulf of Mexico shrimp fisheries averaged slightly more than 171 million pounds worth about 56 million dollars to Gulf coast fishermen (U. S. Fish and Wildlife Service, 1962b, 1963b, 1964a). Roughly 17 percent of this volume originated in extraterritorial areas off the Mexican coast. The remaining 143 million pounds from United States waters is a conservative estimate because it does not include appreciable but unknown quantities taken for private use as food and bait.

Most shrimp taken commercially from the Gulf are stored and distributed in a frozen state, the remainder being canned, dried, or marketed fresh locally. In addition, increasingly large amounts are sold alive or dead as sport fishing bait (Inglis and Chin, 1959).

In general, the outlook for Gulf shrimp fisheries appears fairly good—provided, of course, that domestic stocks can be maintained at present or perhaps slightly higher levels. This observation does not imply, however, that Gulf shrimp fishermen will not be forced into a progressively more competitive position in the world shrimp market. At present domestic production contributes less than 50 percent to the total United States supply of shrimp (Table 1), with about four-fifths of this internal production—35 to 40 percent of the total supply (1960–63)—originating in Gulf waters (Table 3). Prevailing opinion is that the major stocks of shrimp in the Gulf cannot be safely (or economically) fished to a greater degree than has been achieved in recent years. Consequently, only the development of presently unutilized species offers the Gulf coast shrimp industry any immediate prospects for expansion to meet the growing national demand for shrimp and shrimp products. Regardless of whether such expansion materializes, however, governmental agencies which share such responsibility can be expected to take whatever steps may prove necessary to protect all of the Gulf's shrimp resources from the adverse effects of man's activities, be they in the form of exploitation itself, or of gradual destruction of habitat.

ONTOGENETIC–ESTUARINE RELATIONSHIPS

For all practical purposes, we are concerned only with representatives of two groups of decapod Crustacea, namely, the caridean and penaeidean shrimps. Species of the Caridea, in which the female bears her eggs externally and the young hatch at a comparatively advanced stage of development, are of somewhat minor importance commercially, contributing on the order of 15 percent to the world catch of shrimp, and but 5 percent to United States landings. Penaeids (Family Penaeidae), in which the eggs are released directly into the water and hatch quickly into precocious young, are the real shrimps of world commerce, being usually in greater abundance, more readily accessible, of larger average size, and therefore of higher value.

In general, stocks of carid species support the shrimp fisheries of boreal seas. Prime examples are: (1) the deep-water fisheries

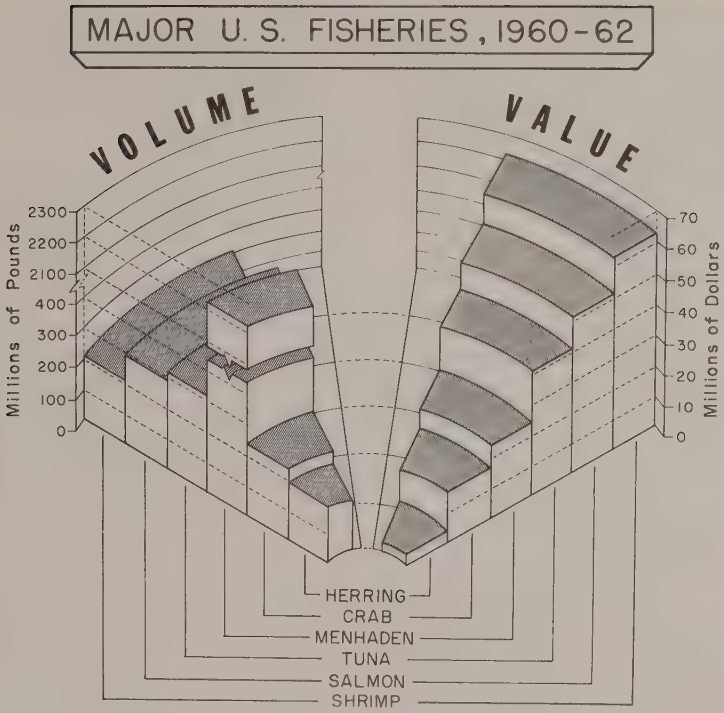

Figure 1.—Average annual volume and value of landings in major United States fisheries during the period 1960–62.

for *Pandalus borealis* in the North Atlantic off New England, Newfoundland, Greenland, and Scandinavia (e.g., Scattergood, 1952; Smidt, 1965), and for *P. jordani* off the Pacific coast of North America (Tegelberg and Smith, 1957), and (2) the shallow-water fisheries for *P. montagui* along the East-Anglican coast (Mistakidis, 1957), for *Crangon vulgaris* off western Europe (Tiews, 1954), and for *Crago franciscorum* in San Francisco Bay (Israel, 1936). Only in the biology of the latter three species do estuaries play an important role.

As a rule, the more prolific of the penaeid shrimps are closely associated with brackish, shallow-water environments. Upwards of 35 species, each with a different and somewhat restricted geographical distribution, support important coastal fisheries throughout the tropical and subtropical regions of the world. Isolated or overlapping stocks of these species are harvested commercially along the coasts of South America, Central America, Mexico, southern Europe, and northern Africa; almost everywhere in the Indo-Pacific area and in Oceania; off China, Korea, and southern Japan; and along the Atlantic and Gulf coasts of the southeastern United States (e.g., Lindner, 1957; U. S. Fish and Wildlife Service, 1958a and b).

The penaeids of commercial significance occurring in the last-mentioned region include the brown shrimp, *Penaeus aztecus*; the white shrimp, *P. setiferus*; and the pink shrimp, *P. duorarum*. Brown shrimp stocks yield about three-fifths of the overall catch of shrimp, with the other two species contributing about one-fourth and one-seventh, respectively. Approximately the same proportions also hold for Gulf fisheries, which produce by far the bulk of shrimp taken commercially in all areas of the region (Table 3). No caridean species of value enter this catch.

Of particular interest from conservational as well as purely biological points of view is the fact that most penaeid shrimps of commerce have a distinctive life history characterized by a period of more or less predictable length which is passed in an estuary or comparable brackish environment (*see* Weymouth, Lindner, and Anderson, 1933; Burkenroad, 1934, 1939; Pearson, 1939; Hudinaga, 1942; Williams, 1955; Hall, 1962). In each of the species so involved, the parent population, breeding in the sea at various distances from the mainland, produces seasonally large numbers of microscopic, semibuoyant eggs which almost immediately hatch into small, planktonic nauplii. Development proceeds rapidly through the protozoeal and mysis stages, the larval shrimp all the while moving or being transported landward in a still-unexplained manner toward the mouths of rivers, or to passages into broad and shallow estuaries. The amount of time lapsing between hatching offshore and entry of the small shrimp into brackish waters inshore may vary from a few days to several weeks, again depending on the species as well as on prevailing oceanic conditions. In the case of Gulf of Mexico forms, namely, the brown, white, and pink shrimps, it is believed that usually 3 to 5 weeks have elapsed by the time the young begin to arrive in the bays as half-inch postlarvae, which no longer may be classed as true plankters. Once in the brackish water of estuaries, the postlarvae quickly transform into juveniles. Over the subsequent 2 to 4 months they grow rapidly and reach commercially acceptable size shortly before their return to the sea where the life cycle is completed.

Appreciable variation occurs among the commercial Penaeidae of the world, both in the degree to which each species utilizes an estuarine-type environment during its life history and in the distribution of its parent population along the brackish-marine gradient of the littoral zone at the sea's edge. Figure 2 illustrates how the more important penaeids generally differ from each other in these respects. The width of the spiral indicates the comparative length of time each new generation spends during early development in an estuary. A point on its axis represents the relative location of the species' parent concentration on the Continental Shelf along the environmental gradient from minimum "brackishness" and maximum fertility to true marine conditions. Information employed in the construction of this figure was drawn from various published sources.

Thus, a subspecies of the greasy-back prawn of eastern Australia, *Metapenaeus mastersii*, completes its life cycle wholly within the confines of an estuary (Morris and Bennett, 1951), while the scarlet prawn of the Atlantic Ocean (and Gulf of Mexico), *Plesiopenaeus edwardsianus*, undergoes entire development in the ocean at depths approaching 900 meters (Springer and Bullis, 1956; Maurin, 1965). In between may be noted all shades of difference in the ontogenetic-estuarine relationship. Fishable stocks of the valuable brown shrimp in the Gulf of Mexico, for example, reach maximum density some distance offshore (off the Louisiana-Texas coast) at depths of from 55 to 75 meters where most spawning occurs (Kutkuhn, 1962; U. S. Fish and Wildlife Service, 1963a). Accordingly, the young upon hatching have a fairly great distance to traverse before reaching the estuaries and, once there, remain only a comparatively short time (Figure 2). In contrast, adult white shrimp are rarely found at depths greater than 35 meters, well within that part of the littoral zone measurably influenced by land drainage. Their young not only spend more time in the estuaries, but penetrate them to a greater degree as well (Burkenroad, 1934; Lindner and Anderson, 1956). Similarly, the seabob, *Xiphopeneus kroyeri*, a small species that in some years may contribute as much as 2 percent to the total United States harvest of Gulf shrimp (Kutkuhn, 1962), completes its life cycle within a very narrow zone lying against the coast. The young do not penetrate estuaries as deeply, nor do parent stocks concentrate as far offshore as their white shrimp counterparts (Burkenroad, 1934; Neiva and Wise, 1964).

The significance of the above information is best appreciated when one speculates on the fate of estuary-dependent shrimps in the event they are deprived of estuarine habitat. The basic question being asked by groups advocat-

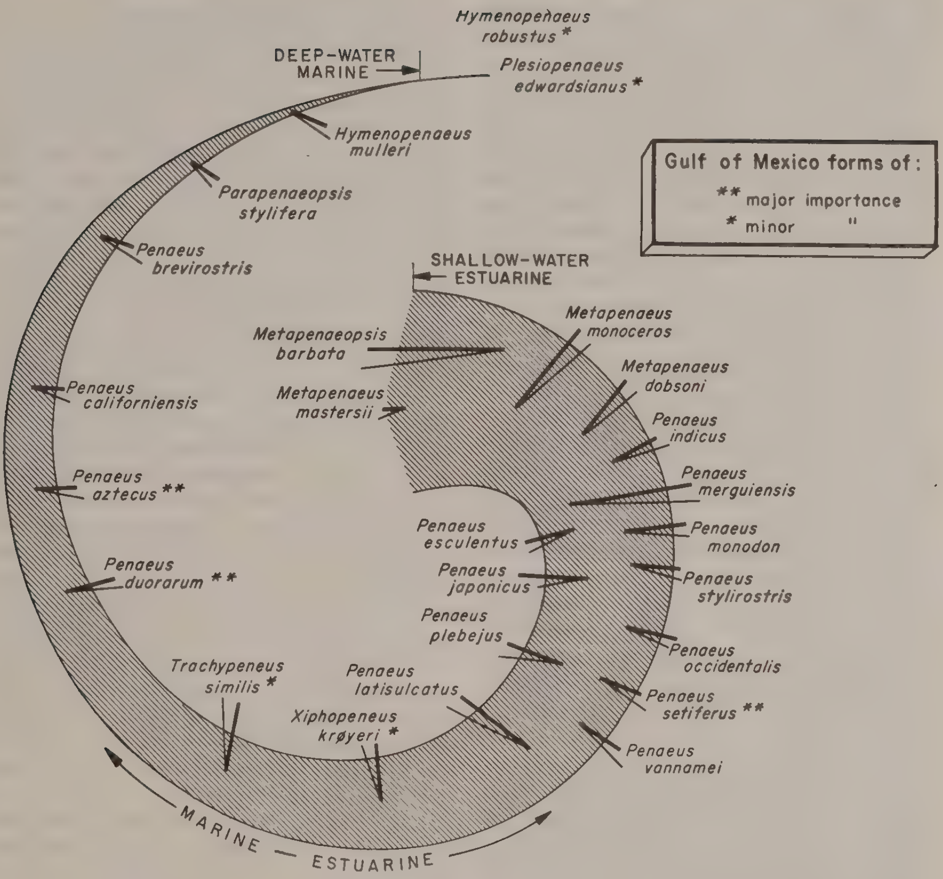
Hymenopenaeus robustus *
DEEP-WATER MARINE
Plesiopenaeus edwardsianus *
Hymenopenaeus mulleri
Gulf of Mexico forms of:
** major importance
* minor "
Parapenaeopsis stylifera
Penaeus brevirostris
SHALLOW-WATER ESTUARINE
Metapenaeus monoceros
Metapenaeopsis barbata
Metapenaeus dobsoni
Penaeus californiensis
Metapenaeus mastersii
Penaeus indicus
Penaeus aztecus **
Penaeus merguiensis
Penaeus esculentus
Penaeus monodon
Penaeus duorarum **
Penaeus japonicus
Penaeus stylirostris
Penaeus plebejus
Penaeus occidentalis
Trachypeneus similis *
Penaeus latisulcatus
Penaeus setiferus **
Xiphopeneus krøyeri *
Penaeus vannamei
MARINE — ESTUARINE

FIGURE 2.—Various penaeid shrimps of world commerce arranged arbitrarily in accordance with the expected degree to which each species inhabits an estuarine environment during its ontogenetic development. The relative position of each shrimp in the estuarine-marine spectrum was either based on the findings of specific life history studies, or inferred from scattered biological observations documented in numerous technical reports. (See text.)

ing development of estuarine areas at the probable expense of the living resources they contain is: Outside of complete reclamation of a system of estuarine basins, won't fishery resources such as shrimp adjust to the new conditions wrought by our activity? And, if not, why not?

Unfortunately, scientists are not yet in a position to answer either question satisfactorily. It stands to reason, from the material presented above, however, that any unusual disturbance of the physical and chemical constitution of an estuarine system would almost certainly be manifested in subtle changes in each species' capacity to achieve a biomass equivalent to that attained under environmental conditions characterizing the ecological niche into which the species has evolved. Abrupt modification of their respective niches would, superficially speaking, affect every species to a different degree.

With the imminent erosion of the estuarine biotope, the question of whether or not the more valuable species can adapt, overnight so to speak, to new combinations of environmental conditions considerably different from those experienced during their evolution is indeed a logical if not an urgent one. In the past certain species of value to mankind have adapted to what were first believed for them to be hostile environments. Others have gradually disappeared from the scene. Who's to say what will materialize in the case of shrimp? Majority opinion is that the fertile estuary, from the ontogenetic point of view, constitutes an irreplaceable factor in the survival strategy of major shrimp resources, and that the perpetuation of such resources *at commercial levels of productivity*, apart from their continued existence *per se*, will be contingent upon our ability to minimize disturbance of the shrimp's estuarine habitat.

Research by various agencies is slowly amplifying our knowledge of the biology and dynamics of shrimp resources at all stages of their life history. But much remains to be accomplished before we can muster the basic information that would provide an unassailable defense concerning the inadvisability of wholesale modification of vitally important coastal marshes.

THE ESTUARY AS SHRIMP HABITAT

The penaeid shrimps of commerce come and go in the manner described simply because that is the way they have evolved. What then typifies the highly dynamic environment occupied during the estuarine phase of their life history? We know when and where the young shrimp (late postlarvae, juveniles, and subadults) occur, and we can grossly describe their surroundings accordingly. But we fall far short of the mark in our ability to define even quasi-quantitatively the *functional* role of the environment.

What are believed to be the major factors regulating the occurrence and development of immature shrimp in the estuarine environment are, in a very general way, briefly described below. Complementing their description are limited discussions concerning present evaluation of cause-effect relationships, and the probable results of temporary as well as permanent changes in environment structure.

Environmental Factors and Biological Processes

Water circulation. Among the more important physical features of the estuarine-marine system are the wind-generated and tidal currents—Chapman (1960) regards the tidal cycle as the "master" factor—which play a large role in making the edge of the sea the highly variable and complex environment we observe it to be. Not only do currents constitute the principal mechanisms by which interchange of fresh and salt water is effected in the estuary (Ketchum, 1953), but the resulting circulation patterns also govern the distribution of: (1) other chemical components of the water in addition to salt content; (2) physical properties such as temperature; (3) suspended matter; and (4) biological populations, especially of those species whose early life history in the estuary entails one or more passive, planktonic stages.

Because of their very dynamic nature, circulation patterns in the estuary, let alone those on the Continental Shelf are not well understood and are therefore largely unpredictable. Much of the work accomplished in this area has been along theoretical lines with that reported by Ketchum (1951), Pritchard (1952a and b, 1955, 1959), proving particularly useful in studies concerning the ecology of estuarine resources.

The most significant advances in estuarine hydrology, from a practical standpoint, have been made by the U. S. Army Corps of Engineers through its extensive waterways experiment program. Procedure here consists of building accurate, small-scale models of specific estuarine basins and, on a trial-and-error basis involving simulated flow and exchange of fresh and salt water, determining how a change in basin configuration, the erection of a public works structure, or the introduction of pollutants will most likely affect an estuary's physical and chemical regimen. Successful models have included the San Francisco Bay (Calif.), Vermilion Bay (La.), Lake Pontchartrain (La.), Charleston Harbor (S.C.), Delaware Estuary, and Narragansett Bay (R.I.) systems. Agencies and persons, other than those interested solely in their engineering implications, have benefited from the results of the many experiments conducted with such models (e.g., Pritchard, 1954). Fishery scientists especially have gained an understanding of the transport systems characterizing those estuaries and, as a consequence, are in a better position to prejudge how modification will affect, directly or indirectly, the productivity and general well-being of the valuable biological populations they influence (e.g., U. S. Fish and Wildlife Service, 1962a).

Current patterns on the Continental Shelf probably govern in large degree, ostensibly through distribution of the planktonic larvae during the oceanic phase of the shrimps' early life history, the eventual occurrence of postlarvae at the entrances to brackish-water nursery areas. To ascertain the role of ocean currents in the movement of young shrimp from offshore spawning grounds to inshore bays and marshes, the Bureau of Commercial Fisheries is now engaged in a broad, continuing survey of oceanic circulation in the northern Gulf of Mexico (U. S. Fish and Wildlife Service, 1963a and 1964b). Another investigation by the same agency is concerned with evaluating the effects of tidal currents as they facilitate or impede the movement of postlarvae into coastal wetlands. Throughout the young shrimps' occupancy of the estuary, however, there can be little question that circulation *per se* is the key process which, varying in pattern and degree from system to system, establishes indirectly the limits of environmental suitability in terms of temperature distribution, salinity, turbidity, nutrient levels, pollution, etc.

Temperature. Perhaps the pre-eminent environmental factor limiting productivity at all levels of the estuarine food chain is water temperature. Its importance in the case of Gulf coast shrimp resources is inferred from the simple observation that (despite evidence of measurable year-round spawning activity in some species) it is mainly just prior to or during the warmer months when the bulk of the larvae produced offshore enter the estuaries as postlarvae, and subsequent growth of the young shrimp in the bays is most rapid (e.g., Gunter, 1950; Lindner and Anderson, 1956; Baxter, 1963; St. Amant, Corkum, and Broom, 1963; U. S. Fish and Wildlife Service, 1963a and 1964b). Overall, it appears that the situation in these months is generally conducive to the attainment of greatest biomass by a given generation of shrimp. But, to specify an optimum temperature range for the shrimps' brackish-water phase of development, as well as a quantitative measure of the expected long-term effects on shrimp populations of their exposure as postlarvae and juveniles to permanently altered temperatures is quite another matter.

At various stages during their sojourn in Gulf coast estuaries, the young of commercial penaeids have been observed at water temperatures ranging from near freezing to slightly above 95 F (U. S. Fish and Wildlife Service, unpublished data). At levels of 40 F and lower, mass narcosis and mortality frequently occur (Gunter and Hildebrand, 1951; U. S. Fish and Wildlife Service, 1964b). On the other hand, significant increases in shrimp biomass are not generally evident until the temperature reaches 70 F (St. Amant, Corkum, and Broom, 1963). Although the exact nature of their fate when exposed to high temperature is unknown, shrimp taken from waters exceeding 90 F are usually flaccid and highly sensitive to stresses induced by handling. Under extreme temperature conditions salinity and oxygen tension doubtlessly play important roles in controlling the survival of young shrimp.

Salinity and other chemical properties. One of its most variable yet easily measured attributes, salinity probably more so than any other property, characterizes the estuary (Pritchard, 1952). As implied earlier, it is something of a tribute to the penaeid shrimps and other forms similarly adapted that they have evolved with the capacity to endure wide ranges of salinity. Consequently they can take advantage at the most appropriate stages in their ontogeny of the high-nutrient reservoir represented by many estuaries. Other environmental features with which the shrimp are intimately associated while in the estuary—the quality and quantity of phanerogamic vegetation, for example (Chapman, 1960)—may be affected more by salinity differences than shrimp. Thus salinity is a property affecting indirectly as well as directly the shrimps' well-being in estuarine nursery areas.

Penaeid shrimps, at one life history stage or another, have been observed in waters ranging in salinity from less than 1 (Gunter, 1956; 1961) to more than 60 parts per thousand (Gunter, Christmas, and Killebrew, 1964). Salinity optima for the young of commercial varieties found in estuaries along the United States Gulf coast are believed to vary from about 5 to 20 ppt (Gunter et al., 1964).

Much less is known about the spectra (as they relate to shrimp distribution, growth, and survival) of other chemical constituents distinguishing estuarine waters in which the polybiotopic shrimps are known to occur. Some data on dissolved oxygen, various nitrogen and phosphorus ions, vitamins, etc., may be found in the literature but they are so specific, scattered, or incomplete as to be either useless or meaningless. Perhaps the major reason for the sketchiness of such data is the highly ephemeral or capricious nature of many of these properties.

Pomeroy (1960), for example, attributes the very short residence time of dissolved phosphates to their rapid rate of turnover, which he notes is not only independent of but probably more important than phosphate concentration in maintaining good production in a given ecosystem. Similarly, Starr (1956) showed that detritus in water flowing from *Spartina* marsh immediately following high slack tide contained far more vitamin B_{12}, an important growth-promoting factor, than did detritus in water collected somewhat later in the same tidal cycle. These observations point up the general futility of taking anything other than the most systematic of measurements in attempts to establish cause-effect relationships between such properties and the biological populations they interactively control.

Turbidity and fertility. Also of great importance from a biological viewpoint is the relative degree to which the estuary's water column is penetrated by light. Obviously, the horizontal as well as vertical distribution of luminous energy in any body of water depends upon the quality, density, and areal extent of the suspended organic and inorganic matter it contains. Despite the consistently large amounts of seston in many inshore areas, marked attenuation of light at any depth is rarely considered a factor impeding attainment of the high basic productivity typifying most estuaries, especially the very shallow ones bordering much of the Gulf of Mexico.

Still largely unresolved is the issue concerning the relative contribution of allochthonus materials and processes to the fertility of estuarine systems. Many elements (and biochemical mechanisms) collectively defining estuarine fertility may have their origin outside the estuary. Implying opposition to this opinion are statements by Odum (1961) and Schelske and Odum (1962) who, though recognizing estuaries as "nutrient traps," rank near the top of their list of factors responsible for high estuarine productivity: ". . . abundant supplies of nutrients . . ." which they maintain *are not* introduced through land drainage. Estuaries do serve as efficient "nutrient traps" through containment of dissolved and particulate matter by tidal action, but they also constitute basins in which nutrients and other essential elements are first entrapped and concentrated, and then promote through recycling the high productivity that distinguishes them.

The point is that estuaries are not closed, self-contained ecological systems. Their production of organic matter is as dependent on material contributed from land and sea as is their brackishness. The salt content of estuaries is regulated by the differential exchange of waters from the open sea on the one hand, and from extensive watersheds on the other, and so is their fertility controlled in large measure by allochthonus nutrients from the sea and, more importantly, from the land. Odum's (1961) views notwithstanding, there exists no tangible evidence that appreciable reduction in freshwater discharge and its "nutrient" load would not, in time, seriously impair estuarine fertility.

No successful studies have been conducted to relate turbidity with shrimp occurrence and density, but gross observation suggests that those bays which are consistently the most roily generally harbor per unit area and in season the largest concentrations of young shrimp. Whether this reflects more the nutritive potential of the detrital material in suspension, or protection of transient shrimp from predation by fishes, birds, and other animals, remains a moot question. Results of investigations by Williams (1955), Flint (1956), Darnell (1958), and Hall (1962), among others, suggest that such material may serve in this dual capacity.

To the extent that the estuary's planktonic flora provides food for the young omnivorus shrimp, a gradual reduction of light at all levels of the water column, due, for example, to a steadily increasing silt load, could be expected to suppress algal productivity in open bay waters (Ragotzkie, 1959) and thereby indirectly inhibit the development of shrimp biomass. In most estuaries of interest here, however, it is highly improbable that such a decline in the algal food source would, by itself, significantly reduce their carrying capacity for shrimp.

Vegetation. Estuaries along the northern Gulf coast characteristically contain large amounts of suspended material and hence exhibit comparatively limited growth of submergents. Emergent vegetation on the other hand is usually well developed at the edge of bays, and especially so in their surrounding marshes. It is such areas—the shoreline zone and transitional marsh, typically vegetated with mangroves or with rushes, reeds, cane, and various grasses, particularly *Spartina* and *Distichlis*—that are sought by the young of most penaeid shrimps during the earliest stages of their estuarine existence, presumably for protection and food. Significantly, it is also the same areas which, through reduction of their vegetative cover due to chronically high salinity, would very likely be subject to gradual, widespread deterioration in the event freshwater inflow is decreased appreciably by one means or another (Chapman, 1960). The consensus of those investigating the biology of commercial penaeids is that the importance of the vegetated shore zone-marsh habitat surrounding most estuaries cannot be overemphasized.

Substratum. One other environmental factor meriting at least passing attention is the estuary's bottom structure as related to shrimp distribution. Repeated observations by fishermen have aroused speculation regarding its role in governing the carrying capacity of the commercial shrimps' estuarine nursery grounds. But not until fairly recently has anyone attempted to demonstrate statistically that a relationship between bottom type and shrimp distribution may exist.

Williams (1958) showed by means of carefully designed laboratory experiments with the three major commercial species of the northwestern Atlantic and Gulf of Mexico, that the pink shrimp selected most often the comparatively hard substrate of mixed shell and sand; the brown and white shrimps occurred most frequently on softer bottoms composed of loose peat, sandy mud, or muddy sand. His experiments suggested that protective cover rather than food content was the primary attractant. From this limited information one may reasonably conceive that a gross change in substrate composition, arising, for example, from an increased silt load or a reversal in circulation pattern, with attendant changes in scouring action and rate of sediment deposition, could alter estuarine carrying capacity.

Response to Environmental Change

One finds it difficult to refute the conclusion that all the above factors, among a host of unspecified others, play complex interactive roles in determining the distribution, survival, and growth of young shrimp during their occupancy of the estuary. Yet, useful evidence of the mechanics involved, and of the extent to which changes in these factors influence the overall productiveness of commercial shrimp resources, is conspicuously lacking. So-called ecological investigations in numerous estuaries renowned as shrimp nursery areas have accomplished little more than detailed descriptions of the flora and fauna, and of the general features of the estuarine environment as a habitat for young shrimp. Apparently, specification of cause-effect relations between the brackish environment and the well-being of shrimp resources inhabiting it awaits the development of suitable mathematical and experimental techniques. The usefulness of such tools in furnishing guideposts so badly needed in the prejudgment of public works projects and other cultural activities that promise impairment of estuaries and surrounding marshes may be readily envisioned.

Most research in the area of environment-induced stress on populations of shrimp has been performed through small-scale laboratory experimentation under simulated, carefully controlled conditions. Activity so far has ranged from attempts to explain the physiological mechanisms that permit young shrimp to adjust almost immediately to changes in salinity and temperature, to measurement of their general tolerance to temperature and salinity over a broad spectrum. Pannikar (1951) gives a useful introduction to the topic of regulatory capacity in estuarine-marine fauna (including penaeid shrimps), and its meaning from evolutionary as well as ontogenetic points of view.

In the case of physiological adaptation, Williams (1960) demonstrated experimentally that between 20 and 25 C the internal fluids of juvenile and subadult brown and pink shrimp have a lower osmotic pressure than the external medium when in ordinary sea water; they are hypertonic when the sea water is diluted to 30 ppt or less. He observed, too, that the shrimps' regulatory ability diminishes below 9 C, their blood tending toward isotonicity in the process. His findings also indicated that the pink shrimp is a better regulator at low temperatures than the brown shrimp, and that survival of both species under such conditions is probably best when the salinity is high. Similarly, McFarland and Lee (1963) concluded that subadults of brown shrimp and white shrimp adjusted their salt content hypo-osmotically in sea water, and hyperosmotically in a hyposaline environment. In contrast, stenohaline penaeids such as *Trachypeneus similis* and *Sicyonia brevirostris*, which ordinarily do not enter the estuary at any stage in their development, are slightly hypo-osmotic in sea water but succumb rapidly as salinity decreases.

Dobkin and Manning (1964), working with an estuarine and a freshwater species of the caridean genus *Palaemonetes*, determined that the estuarine form maintains constant osmotic concentration over a salinity range of 0.6 to 39.0 ppt, which indicates its blood is hypotonic in a concentrated medium and hypertonic in a dilute medium. The freshwater form proved hypertonic over the range of salinity to which it is normally exposed, with its regulatory capacity breaking down at salinity levels in excess of 20 ppt. Broekema (1941) observed essentially the same characteristics in the common European shrimp, *Crangon crangon*, also a caridean species. In addition, he found that the difference in salt concentration between this shrimp's internal fluids and its environment increases with temperature.

Rao (1958) complemented these findings by demonstrating that oxygen consumption in *Metapenaeus monoceros*, a commercially important shrimp of the Indo-Pacific region, increased as the salinity of the experimental medium was reduced below that of the normal habitat. Two groups of shrimp were involved, one from brackish water, the other from the adjoining marine environment, and in each the percentage increase in oxygen consumption was clearly related to the osmotic difference between body fluids and test medium. Upon prolonged exposure to lowered salinity, however, the oxygen uptake gradually returned to "normal," indicating operation of a homeostatic mechanism actuated by osmotic stress.

Although they impart considerable understanding as to how polybiotopic shrimps adjust physiologically to a varying environment, these observations provide little more than a basis from which the effects on resource productivity of long-term upward or downward trends in temperature and salinity might be conjectured. Of current widespread interest is not so much an answer to the question of why and how these organisms can cope satisfactorily with their dynamic environment, but rather to what degree might the magnitude of their stocks be affected by permanent environmental changes.

Studies to resolve this question are underway at the Bureau of Commercial Fisheries Biological Laboratory in Galveston, Texas. Bureau biologists have demonstrated that tolerance to salinity of postlarval and juvenile brown shrimp narrows perceptibly at reduced temperatures. Other findings provide evidence not only of the ability of young shrimp to adapt readily to a broad spectrum of temperature-salinity conditions, but also of their ability to select suitable conditions so as to avoid osmotic situations involving undue physiological stress (U. S. Fish and Wildlife Service, 1963a and 1964b).

Experiments by Zein-Eldin (1963) indicate that rates of growth as well as survival in postlarval brown and white shrimp, with all other factors remaining constant, may not change significantly between salinities of 2 and 40 ppt. More recently, Zein-Eldin and Aldrich (1965) have confirmed the results of earlier growth and survival experiments in which brown shrimp postlarvae were shown to be capable of adjusting to a wide range of temperature-salinity conditions. They concluded, however, that higher levels of salinity are probably more favorable than lower ones as temperature limits are approached; growth, although good at all levels of salinity, is best within a somewhat narrow temperature range.

Of growing concern is our lack of information about the immediate or gradual fate of shrimp upon exposure during their estuarine phase to ever-increasing pollution. This offensive index of man's progress may be conveniently separated into three general categories on the basis of origin, namely, domestic, industrial, and agricultural.

Recent (unpublished) observations by Bureau of Commercial Fisheries personnel in Galveston Bay (Tex.) suggest that at least up to a certain level the presence of domestic wastes may be beneficial owing to the added fertility they bring to the environment. But explicit investigation of the effects of increased domestic pollution on concentrations of young shrimp in the estuary probably has not yet been attempted. Nor have the conceivable effects of chronic industrial and agricultural pollution been studied. Numerous laboratory experiments in which young shrimp were subjected to various dilutions of an industrial waste (Pulley, 1950), a mosquito-control chemical (Chin and Allen, 1958), and a variety of agricultural pesticides (U. S. Fish and Wildlife Service, 1959b, 1960, and 1961) suggest, however, that even at very low dilutions, many pollutants in these categories are lethal to shrimp. A major impediment to field assessment of the true consequences of their prevalence in the estuary is our inability to identify and measure these toxic compounds (or perhaps their degradation products) with reasonable accuracy.

From the standpoint of the commercial shrimps' evolution and of their possible fate, the implications of preliminary information like that outlined above are fairly clear. Certainly, more research of this type is necessary, especially that treating other important environmental variables such as organic salts, turbidity, and food supply. Nevertheless, the work completed to date is providing needed direction for meaningful pursuit of ecological (cause-effect) relationships. The demand for information of this kind, with which to defend the maintenance of our estuaries as a necessary environment for biological resources of commercial and recreational importance, is becoming increasingly desperate. Consequently, attempts to translate even preliminary laboratory results into predictive techniques seem justified.

Natural Adversities

In the foregoing section attention was turned primarily to the general problem of forecasting the likely response of commercial shrimp resources to the very gradual or more subtle environmental changes that might be anticipated as an outgrowth of man's wholesale assault on the estuary. The development of mathematical models, employing ecological data which, in turn, are given direction by laboratory research was posed as a possible solution to this problem.

Not nearly so easily resolved are the consequences of unpredictable, largely infrequent, but often precipitant meteorological events. Included here are droughts, flooding due to heavy stream discharge, freezes, and tropical storms. The shallow estuaries and their biological populations are particularly prone to the effects of these occurrences. Unfortunately, only speculative information exists as to the real nature and extent of such effects. But it is evident that they would, in almost every case, be expressed initially in the abrupt change of one or more of the environmental properties discussed earlier.

Droughts. On the question of extended droughts and their relation to the annual productivity of commercial shrimp resources, the works of Hildebrand and Gunter (1953), Gunter and Hildebrand (1954), Parker (1955), and Viosca (1958) have perhaps stimulated the most thought. In each instance the species involved was the white shrimp which prior to 1948 constituted the mainstay of the Gulf coast shrimp industry. Whereas Viosca (op. cit.) merely conjectured the drought of the late 1940's and early 50's as being the principal cause for the sharp decline experienced by the white shrimp fishery of Louisiana and Texas during that period, the former two authors attempted a statistical correlation of annual white shrimp harvests with corresponding measures of precipitation. Their analyses suffered, however, due to inadequate fishery statistics and the inability to establish satisfactorily a functional relationship between resource productiveness and estuarine salinity.

Because of the young white shrimp's seemingly greater propensity for less brackish water than displayed by other species, it was assumed that higher estuarine salinities resulting from the drought caused environmental stress, reduced habitat carrying capacity, and therefore meant for this shrimp a lower annual biomass and yield. Such an assumption appears sound. But, as in the case of the shrimps' other environmental requirements, the salinity factor awaits experimental assessment in terms of its relative importance both alone and interactively with others.

Conversely, the sudden discharge into estuaries of greater-than-normal amounts of fresh water arising from heavy precipitation on upland watersheds could be viewed as beneficial. This was the position taken by Viosca (1938) who observed that the harvest of white shrimp from Lake Borgne and Mississippi Sound (La.) in 1937 (a year when a great volume of spring flood waters was diverted through the Bonnet Carre spillway into Lakes Pontchartrain and Borgne) exceeded the landings of any previous year. His rationale for this upsurge in shrimp abundance and fishing success paralleled that stated above, but it was tempered by the possibility of the increased amounts of nutrient material carried by the flood waters into the estuaries.

Working in Australia with five penaeids similar in life history and habits to the Gulf of Mexico white shrimp, Thomson (1956) correlated their combined annual harvest and the amount of rainfall in various combinations of preceding units of time. He concluded on the basis of 17 years of observations in the Lake Illawarra region of New South Wales that: "The greater the rainfall of the previous two years the greater the prawn catch is likely to be." He did not venture an explanation of the mechanics involved.

So far as is known no other attempts have been made to demonstrate analytically the general effects of droughts and floods on the productivity of commercial shrimp resources.

Tropical storms. Even less attention has been directed toward evaluating the short-term but potentially disastrous influence of severe tropical storms on shrimp stocks. In ascribing causes of the sharp (55-percent) drop in the harvest of white shrimp from Louisiana waters in 1957, Kutkuhn (1962) considered the likely effects of two hurricanes, one of great intensity, which struck the Louisiana coast in late June and early August, respectively. The reasoning provided is as follows:

"The occurrence of these storms coincided with periods of peak (estuarine) and near-shore concentrations of (1) migrating juveniles representing the 1956 late-season brood, and (2) late postlarvae and juveniles representing the 1957 early-season brood. Although the mechanics involved are obscure, it is conceivable that factors such as: extended periods of high salinity, destruction of cover and food supplies, and excessive turbulence, all induced by extraordinarily high tides, acted corporately to disperse and otherwise exert greater-than-normal mortality in white shrimp populations during vulnerable (estuarine) phases . . . ."

Freezes. Among the regions of the world harboring commercial shrimp resources, only along the Gulf and South Atlantic coasts do abnormally low temperatures in estuaries and nearshore waters possibly influence shrimp supplies. Two factors appear equally responsible for this recurring problem: (1) the prevalence of sizable stocks of penaeid shrimps near upper latitudinal limits for the tropical and subtropical (littoral) Penaeidae, and (2) the unique geography of the coastal region involved, which leaves it exposed to the full impact of polar fronts that sweep from north to south across North America.

The occurrence and immediately observed results of many freezes along the Texas coast have been recorded (Gunter, 1952) but none has prompted more discussion than those of the freeze of January 1940. Upon this widespread, intense, and protracted cold spell was blamed the mass mortality in Texas of thousands of pounds of fishes and invertebrates, including some shrimps of commerce, although adverse effects in terms of subsequently reduced shrimp supplies and commercial harvests never became evident (Gunter, 1941 and 1945; Gunter and Hildebrand, 1951). Lindner and Anderson (1956) reported a virtual loss of the white shrimp resource along the South Carolina and Georgia coasts in 1940 due, presumably, to the same cold wave. An explanation for the apparent geographical variation in the consequences of this uniformly widespread freeze has never been set forth, but it is significant to note that its observed effects in the case of commercial shrimps were short-lived as attested by the Carolina–Georgia fishery's return to normal the following year.

The susceptibility of fauna in Gulf and South Atlantic estuaries to the harmful influence of freezes is logically attributed by Gunter and Hildebrand (1951) to a combination of factors, the most important of which are the shallowness of the water, hence its capacity to cool quickly with the sudden passage of a cold front, and the restricted openings of many bays and bayous that impede the egress of organisms to avoid the rapidly dropping temperatures.

Modification by Man

If basic relationships between the physicochemical features of the estuarine environment and the well-being of its biological resources are poorly understood to begin with, then it follows that we can neither fully appreciate nor predict the overall impact of permanent changes in these features due to man's cultural activities. Although a moderate amount of information has accumulated on the local effects of public works and industrial engineering projects in terms of their physical and chemical alteration of coastal wetlands (e.g., Bourn and Cottam, 1950; Reid, 1956, 1957; Hutton, Eldred, Woodburn, and Ingle, 1956; and Rounsefell, 1964), nothing is known with any degree of certainty about the results of such alteration in terms of changed potential in shrimp and many other estuarine fishery resources.

At the present stage in the development of our knowledge on these matters, we are able merely to describe the general nature of proposed modifications, and to speculate on how they will be (or have been) reflected in the altered productivity of commercial shrimp resources. To save space and unnecessary discussion, I have accomplished these tasks in Table 4, which is self-explanatory.

By way of clarification, it should be pointed out that many of the features listed in Table 4 are interrelated. For example, the dredging of navigation channels, while greatly deepening a limited acreage of a particular bay system, often results in the deposition of spoil banks which may effectively subdivide the system in such a way that subsequent changes in shoaling patterns will render the segmented portions shallower and less useful as nursery area than previously. One may logically reason also that nearly every physical development of the estuary is aimed at enhancing the region involved for purposes of industrialization, urbanization, and other cultural pursuits, all of which can be expected to contribute ultimately, unless checked at the outset, to a pollution problem of enormous proportions and uncertain consequences.

Reference to Table 4 will also indicate the number and magnitude of engineering projects already completed or planned for Gulf coast estuaries. It is doubtful if comparable development of estuarine areas in other shrimp-producing regions of the world exceeds that in the southern United States.

In summary, most of man's engineering activity in coastal lowlands generally affects the estuarine shrimp habitat in two major ways: (1) change in mean salt content and

TABLE 4.—*Various types and likely consequences of man-induced modifications of the estuarine environment as a habitat for the young of economically important shrimps*

Feature	Examples	Expected environmental effects	Probable results in terms of resource productivity	
			Adverse	Beneficial
I. *Change in basin configuration:*				
Bulkheading and filling	Tierra Verde project (Florida); numerous bayside real estate developments (Gulf coast)	General reduction in acreage of desirable shore-zone and marsh habitat; alteration of marsh drainage patterns (e.g., Hutton, Eldred, Woodburn, and Ingle, 1956)	Decreased productivity due to loss of carrying capacity through destruction of plant cover and food sources	None
Dredging of navigation channels and "fish" passes	Intracoastal Waterway (Atlantic and Gulf coasts); Houston Ship Channel (Texas); Mississippi River-Gulf Outlet (Louisiana); Rollover Pass (Texas)	Partial deepening of bays; alteration of marsh drainage patterns; increased exchange of oceanic, bay, and marsh water; change in circulation and hence distribution of salinity, temperature, etc.; temporary increase in silt load (Rounsefell, 1964; Reid, 1956, 1957)	Possible intrusion of greater-than-normal amounts of sea water could decrease carrying capacity of marshes through reduction of plant cover and food sources	Increased carrying capacity through provision of access for small shrimp to previously inaccessible estuarine and marsh areas; deepened areas offer haven or routes of escape from effects of sudden cold fronts
Segmentation by spoil banks as well as by rail- and highway grades	Galveston Bay (Texas); Calcasieu Lake (Louisiana); Tampa Bay (Florida)	Lessening of average bay depth through shoaling due to structures' influence on circulation; reduced exchange of fresh and salt water (U. S. Fish and Wildlife Service, 1963a and 1964b)	Slight loss of bottom acreage, disruption of flow patterns, and impedance of shrimp movements would have nominal effect on productivity	None
Ditching of marshes	Maine to Georgia (Atlantic coast)	Lowered water table; gross change in vegetative cover; loss of nutrient material from marsh areas (Bourn and Cottam, 1950)	Loss in productive potential attributable not only to loss of plant cover and food sources, but to reduction in nursery acreage as well	None
II. *Protective works:*				
Stream-diversion spillways	Bonnet Carre spillway (Louisiana)	Redistribution of freshwater discharge; change in estuarine salinity regimen (Viosca, 1938; U. S. Fish and Wildlife Service, 1959a)	Depending on species, lowered carrying capacity in some areas	Depending on species, increased nursery acreage and hence carrying capacity in some areas
Salt-water barriers	Calcasieu Lake area (Louisiana)	Impeded exchange of fresh and salt water; altered patterns of salinity distribution	Limited reduction of carrying capacity due to loss of marsh habitat	None
Sea walls, dikes, and levees	Galveston Seawall (Texas); proposed hurricane-protection dikes (Texas) and closure of Vermilion Bay (Louisiana)	Restricted influx of salt water; loss of tidal-exchange benefits; change in salinity regimen (U. S. Army Corps of Engineers, 1959; U. S. Fish and Wildlife Service, 1962a)	Generally lowered productivity because of diminished access to broad estuarine areas for young shrimp	None
Tide-control structures	Lake Pontchartrain (Louisiana)	do.	do.	None

TABLE 4.—Continued

Feature	Examples	Expected environmental effects	Probable results in terms of resource productivity	
			Adverse	Beneficial
III. *Change in volume and seasonal distribution of freshwater inflow*	Numerous upstream dams (Gulf coast); proposed Texas Basins project (Texas)	Generally heightened salinity; increased concentration of downstream pollutants; reduced influx of terrigenous nutrient material (Chapman, 1966)	General deterioration of estuarine habitat, a vital link in the shrimps' survival strategy, would mean a measurable loss in productivity	None
IV. *Pollution:*				
Domestic	Galveston and Mobile Bays (Gulf coast); Thames and Elbe estuaries (Europe)	Change in water chemistry; increased biological demand for oxygen	Superenrichment could induce suffocation and loss of productivity	Increased fertility—limited enhancement of productivity
Industrial	do.	Change in water chemistry; presence of toxic or suffocating compounds	In cases of inadequate dilution, decreased shrimp survival and productivity	None
Agricultural (including mosquito-control measures)	Areas producing rice, sugar cane, and cotton (Gulf coast)	Introduction through sheet run-off of pesticides and herbicides (Butler and Springer, 1963)	do.	None
V. *Development of mineral resources:*				
Oil production	Louisiana and Texas (Gulf coast)	Ordinarily slight pollution; segmentation of bays by pipelines (see Item I)	Nominally decreased productivity due to somewhat poorer survival; hindrance to harvest of shrimp most significant result	None
Dredging of fossil shell deposits	do.	Change in bay circulation patterns; increased silt load	Some reduction of bay carrying capacity due to localized loss of shelter and feeding areas	Questionable

chemical composition, and (2) net loss of carrying capacity, particularly through loss of vegetated marshes as contrasted to open bay waters. It is highly problematical whether the estuary-dependent shrimps of commerce can adjust to such modification and still maintain their stocks at economic levels of productiveness.

Aquiculture—"Shrimp Farming"

The culture of shrimps on a commercial scale is receiving wide attention in the United States and in several other countries. The process entails vastly improving the carrying capacity of a comparatively small area of estuarine habitat through manipulation of the numbers of young shrimp involved and the tight control of their biological and, to some degree, their physical environment. Most successful attempts at shrimp farming, whether subsistence fisheries such as exist in certain parts of South America (Allsopp, 1960) and throughout the Indo-Pacific (Hall, 1962), or commercial enterprises like the one being developed in Japan (Fujinaga, 1963), depend primarily on local tides of sufficient height to permit alternate flooding and draining of diked-off areas of swamp or bay. Of nearly equivalent importance are the adaptability to culture of local shrimp species, and the availability of young (seed) shrimp with which to stock the seminatural ponds at the beginning of each growing season. Descriptions of the many facets of shrimp culture as it is practiced in various parts of the world are given by Hudinaga (1942), Delmendo and Rabanal (1956), Kesteven and Job (1958), and Allen (1963).

To date, shrimp culture attempts in the United States have generally met with failure. One or more of the major reasons have been lack of adequate tide differential, difficulty in leasing or acquiring title to submerged lands, and the doubtful capacity of domestic shrimps to develop in quantity to profitable size under seminatural estuarine conditions (Johnson and Fielding, 1956; Lunz, 1956, 1958; Manning, 1963, 1964). Stimulated by ever-increasing interest in the apparent potential of such an industry, however, research on the biological and economic feasibility of shrimp farming in the extensive tidelands of the southeastern United States promises to expand significantly over the next several years. On the basis of work already completed, it appears most likely that the white shrimp will prove the most amenable to commercial culture.

ESTUARINE RESEARCH: FAILURES AND PROMISES

In the preceding sections I have tried to describe what many believe to be the chief ecological factors controlling the growth and survival of valuable shrimp resources in the estuary. Attempts to rank these factors according to their relative importance, and to specify quantitatively their relation to the overall productivity of fishery stocks of interest, were thwarted at the outset, however, by the fact that such information is practically nonexistent. This handicap comes forcefully home to rest whenever fishery administrators or "experts" are faced with the task of prejudging the effects of various cultural changes in estuaries on shrimp and other biological resources.

There is certainly no intent on the part of any conservation agency to stand in the way of progress. On the contrary, such groups are discharging with ever-increasing success their responsibilities to specify—even though in many cases on somewhat shaky grounds—the most probable effects of tideland development, so that steps can be taken to mitigate them through modification of project plans *before* construction begins and irrevocable damage to biological populations occurs. But despite improved cooperation from construction agencies, brought about through public opinion created by a growing realization that valuable natural resources are indeed being threatened, it still remains for us to elucidate the cause-effect relations upon which the conservationist's real defense of these resources must ultimately rest. This observation raises the fundamental question: In our investigation of the estuarine ecosystem, do we have the "problem" areas properly circumscribed and, accordingly, our objectives clearly in mind?

The kind and amount of estuarine research now being performed range from very restricted and basic inquiries on energy flow, sponsored primarily by private institutions, to much broader ecological-hydrographical studies conducted mainly by governmental organizations for the purpose of providing information ostensibly having practical and immediate application. All such activities can be expected to yield results that in one way or another will enrich our knowledge of the estuarine environment and its inhabitants.

But, to what degree do (or will) the results of current work help resolve the grave issue at hand, namely, the unabated deterioration of estuarine habitat by a rapidly advancing civilization? Evidently very little. In many areas, especially in the shrimp-producing areas of the southeastern United States, the carefully planned assault continues, not because the construction agencies deny any appreciation for the multimillion-dollar commercial and recreational fisheries involved, but because conservation officials have not been able to defend in quantitative terms their arguments that engineering projects promise eventually to wreak havoc with these resources. All such projects are predicated on favorable benefit-cost ratios. It therefore follows that unless more tangible (and not necessarily totally unequivocal) testimony in behalf of the estuaries' important biological resources can be produced, the actual net benefits of any project cannot be properly determined.

If it could be stated with some mathematical certainty, for example, that the erection of a particular protective works would create a situation of chronically high salinity, and that over the years this condition in turn would result in a specified annual decline in production from the coastal fisheries affected, then the amount of monetary loss projected might be sufficient to render the benefit-cost ratio unfavorable and thereby impede development of the project, or at least force its redirection. The present-day fishery administrator rarely, if ever, finds himself in such a tenable position.

The difficulty seems to lie not so much in our basic approach to the problem at hand but in our inability to develop the analytical tools to resolve it. The synoptic ecological survey in the field, complemented by controlled experimentation in the laboratory, would appear not only logically sound but realistic and intuitively correct as well. Awaiting the theoretician's skills, however, is the evolvement of autoregression, serial correlation, or other computer-oriented techniques without which the fishery scientist cannot synthesize quantitatively the multitude of concurrent biological, physical, and chemical data he is so carefully accumulating in many areas (Watt, 1964). For populations of shrimp and other transitory estuarine forms, an important prerequisite to such synthesis is a suitable index of net loss or gain in their biomass during the period they occupy the estuary. Statistical comparison of time-series of such a variable with correponding series of environmental factors, singly and in combination, represents one way in which vitally needed information can be obtained. The sustained pursuit of somewhat unrelated investigations (e.g., the "pure" and, in many cases, vaguely directed research on primary productivity in the estuary) by public-supported agencies endowed with the initial responsibility of protecting fishery resources and their habitat appears questionable at this point. The fact remains that the estuarine environment is being changed drastically at an alarming rate, and unless all available and potential support—from research findings to public opinion—can be rallied to check it, anticipated encroachment threatens to nullify the estuary, not only as the producer of desirable food products and the site for a wide variety of recreational activities, but also as the object of scientific curiosity.

In conclusion, current government-sponsored research on shrimp, though rather limited in scale, has as one of its major objectives a working understanding of the functional relation between the shrimp and the collective facets of its estuarine habitat. Unfortunately, progress has been painfully slow and the point has barely been reached where we can say: "We've proceeded far enough descriptively, now let's get on with the analysis of function." For it is solely in the latter area, as sophisticated and costly as our approach may have to be, that our only real defense in insisting upon the perpetuation of our coastal fishery resources can be found.

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Bilateral Asymmetry in Paired Meristic Characters of Pacific Salmon

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ABSTRACT: The presence, extent, and direction of bilateral asymmetries of lateral line scales, gill rakers, branchiostegal rays, and pectoral fin rays of sockeye, chum, and pink salmon were examined. Some asymmetries were found in all characters in each species. Asymmetries, considering all species combined, occurred in approximately 72% of the lateral line scale comparisons, 59% of the gill raker comparisons, 70% of the branchiostegal ray comparisons, and 26% of the pectoral fin ray comparisons. Bilateral variation in these characters was not conclusively related to sex of the specimens; however, some tendency toward greater asymmetry in branchiostegals of females was shown. Complete evaluation of this tendency will require further examination.

Occurrences of asymmetries were evaluated in relation to the reliability of substituting counts from the opposite side when the chosen side was lost or severely damaged. Substitution of lateral line scales of sockeye salmon appeared to be feasible, but in chum salmon the right side counts were significantly greater. (Scale counts from pink salmon were not available, because of the extreme difficulty in obtaining reliable counts of the characteristically small scales.) Gill raker counts from sockeye salmon were found not to be interchangeable, as the right side counts significantly exceeded those of the left. In pink and chum salmon, bilateral variations in gill rakers appeared to be equal. Branchiostegal counts from the left sides of all species were significantly greater than those of the right. It was indicated that, for all species, pectoral fin ray counts from either side could be substituted reliably.

BILATERAL ASYMMETRY in various body parts has been recognized in many animals that have a bilaterally symmetrical form of development. The extent and cause of many asymmetries have not been defined. Asymmetries of fish in the order Pleuronectiformes (flatfish) result in normally dextral or sinistral individuals and have been attributed generally to the processes of natural selection and adaptions of the organism to life on the ocean bottom. Hubbs and Hubbs (1944:303), emphasizing the morphology of flatfish, have pointed out that some asymmetries appear in many body parts of all fishes, both externally and internally. In studies on meristic and other characters of four species of chars, Vladykov (1954:910) has noted somewhat higher gill raker counts on the right sides. In Pacific salmon bilateral asymmetry of branchiostegals, in which the left side overlaps the right anteriorly and contains more rays, has been described by Jordan and Evermann (1896:479).

As a consequence of these known asymmetries in fish, morphological characters from both sides of all species, ideally, should be examined for taxonomic and racial studies, or examination should be limited to one chosen side. If the latter alternative has been adopted, problems arise if the chosen side is mutilated or otherwise unobtainable. In racial studies on Pacific salmon (Fukuhara et al., 1962), data on various meristic characters were arbitrarily collected from the left side of all specimens. The racial study involved multivariate analysis of data from several meristic characters; therefore occasional failures to obtain information from any one lost or damaged character prevented the specimen's use and reduced the usable sample size. As the reliabiilty of the analysis was in part determined by the sizes of samples, unusable specimens were both a statistical and an economic loss.

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Whether asymmetrical development, as shown in the branchiostegals of Pacific salmon, extends in some degree to other paired structures is unknown. With knowledge of the presence and extent of asymmetries in the characters considered, the opposite member of a lost character in fish specimens many times could be reliably substituted; if it were known that such characters essentially developed symmetrically, substitution would not contribute to the observed variability.

This paper presents an analysis of differences between the numbers of elements in left and right side structures of four paired meristic characters of sockeye (*Oncorhynchus nerka*), chum (*O. keta*) and pink (*O. gorbuscha*) salmon. In conjunction with this study, the reliability of the criteria utilized in obtaining the morphological characters will be discussed. The objectives of the analysis were to determine: (1) if bilateral asymmetry occurs in these characters; (2) the extent of asymmetries; (3) the direction of the asymmetrical development, as shown by one side tending to have a larger number of elements; and (4) the usefulness of the information in taxonomic and racial studies of the three species.

SAMPLES

Paired meristic characters were randomly obtained from specimens collected during the years 1956–1959 in the North Pacific Ocean, the Bering Sea, and from several North American and Kamchatkan rivers for racial studies conducted at the Seattle Biological Laboratory, Bureau of Commercial Fisheries. The characters examined included: (1) lateral line scales, (2) total gill rakers, (3) branchiostegal rays, and (4) pectoral fin rays. Lateral line scales of pink salmon were not examined because of extreme difficulty in obtaining reliable counts of the characteristically very small scales.

COLLECTION OF CHARACTERS

The paired bony structures were dissected from the specimens and left and right sides were radiographed separately. When the radiographs did not provide adequate resolution, the structure was stained and cleared, and the elements were counted manually. The data were obtained using criteria developed by Fukuhara et al. (1962: 27–28) for enumeration of characters. The definitions of criteria, elaborated upon below, include discussion of some structural characteristics and aberrancies which must be taken into account during enumeration of the characters. Application of these criteria minimized differences between individual interpretations and the time required for enumeration of the characters. As measured by periodic tests of between-reader variability, disagreements on independently obtained counts from radiographs averaged less than 3% for the bony characters. All scale counts were obtained by one biologist. Within-counter variability averaged less than 2%.

Lateral Line Scales

This character consisted of scales or scale pockets distinguishable by a tube which penetrates the scale and extends into the underlying lateral line canal. The count included the first scale posterior to the pectoral girdle and succeeding scales terminating at a position on the lateral line corresponding to the posterior margin of the hypural plate. This margin was determined by an incision made in the crease that resulted from upward flexion of the caudal fin. A severed scale or pocket was counted if more than half lay anterior to the incision. In immature specimens, acute scale imbrication required scale removal for accurate enumeration. Occasional irregularity of typically diagonal scale rows was caused by a supernumerary scale lying on the lateral line between two scales in the proper rows (Fig. 1). Some of these small scales lacked a tube and therefore were not counted.

Total Gill Rakers

This character consisted of rakers on the dorsal and ventral arms of the first branchial arch, including the most anterior rakers, which were

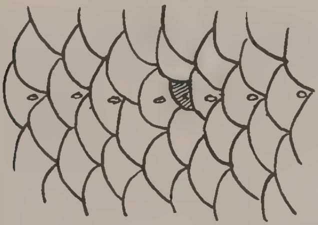

FIG. 1. Supernumerary scale lying on lateral line. Occasionally such scales are not penetrated by a lateral line canal tube.

frequently rudimentary. Rudimentary rakers occurring between the typically uniformly spaced rakers (Fig. 2*a*) and those lying outside the main row were not enumerated. Bifurcated or branched rakers (Fig. 2*b*) with a common base were counted as one raker.

Branchiostegal Rays

All bony elements of the branchiostegal were included in counts of this character. In chum salmon, particularly, the reduced size and modified shape of some anterior rays (Fig. 3) resulted in very deceptive radiographic presentations. In preparation for radiographing, the skin and cartilaginous material anterior to these rays had to be carefully removed to minimize deception. Careful examination was also required for recognition of an occasional ray which appeared as two rays due to the presence of a prominent lengthwise suture. Dissection and staining were used to resolve doubtful conditions.

Pectoral Fin Rays

All fin rays which extended to the basal bones of the fin were included in the character. So-called "floating rays," which occurred in various positions among the normal rays, were not counted (Fig. 4*a*). No counts were taken from fins in which a lateral process arising from one position had fused with a process on the opposite side arising either anterior or posterior to it. This left both a right and a left side process standing alone, as shown in Figure 4*b*.

STATISTICAL PROCEDURES

For each character, the right side counts were subtracted from the left side, differences being positive when the left side counts exceeded the right and negative when the right side counts exceeded the left. The significance of the mean difference between the number of meristic elements in left and right side structures observed in each sample was determined using the Student's t-distribution:

$$t = (X - \mu)/Sx$$

where X equals the mean difference of left side counts minus those from the right side, μ equals zero, and Sx is the standard error of the sample mean difference. The hypothesis tested was that the difference between left and right side counts was zero. The hypothesis was rejected at the 0.05 level. The probability levels of the observed t-values are presented in the tables of data and results.

The extent of over-all asymmetry in each character was measured by the percentage $100(L + R)/N$, and the direction of asymmetry by the percentage of sinistrality $100L/(L + R)$, where L equaled the number of specimens with greater left side counts, R equaled the number with greater right side counts, and N equaled the total sample size, including specimens with equal numbers of elements in the left and right side structures.

Although there was little or no known biological reason to suspect that differential asymmetrical development was related to sex or area of origin of salmon, these possibilities were explored, in so far as the data warranted, for any obvious tendencies of this nature. Actual statis-

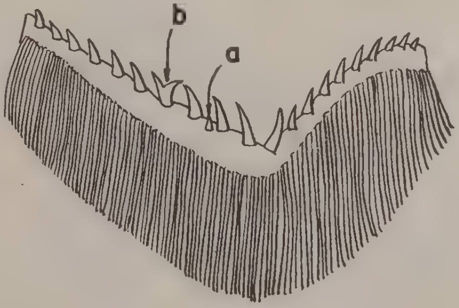

FIG. 2. First left gill arch. *a*, Small raker between regularly spaced rakers on ventral arm of the arch; *b*, a bifurcated raker on the ventral arm.

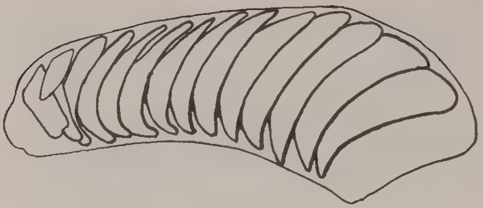

FIG. 3. Chum salmon branchiostegal, showing modified configuration of anterior rays.

tical analyses of between-sex, within-sample, differences were not attempted due to small sample sizes; nor were between-area differences tested for statistical significance, inasmuch as many samples were obtained from the high seas and contained specimens of unknown and perhaps differing origins.

For each sample, probability values associated with the t-distribution for differences between paired counts were obtained by sex. Sexes were then combined and analysed as a single sample. Similarly, for each species, probability values were determined for all males and females separately; the sexes were then combined to determine the mean differences between left and right side structures for comparison among species.

RESULTS

The results of the analyses of observed differences between left and right side structures are discussed for each meristic character. The occurrence, direction, and significance of the mean differences between left and right side counts have been examined by species, sample location, and sex.

Bilateral Variation in Lateral Line Scales

In sockeye salmon (Table 1), the percentages of specimens exhibiting asymmetry in lateral line scales and the direction of asymmetry varied among samples of each sex and among combined samples of both sexes from different locations. As shown by the right-hand column (headed 100 P), the probability values for the observed mean differences were not significant. For the combined samples, males with differences in left and right side counts averaged 69%, and females averaged 65%. Asymmetry between left and right side scale counts occurred in approximately 67% of the total of 395 specimens. The direction of asymmetry indicated that the right side developed approximately 0.12 scales more than the left side. This difference could have occurred by chance alone more than 5 out of 100 times (P greater than 5); thus, the left and right side variations in lateral line scale counts were not significantly different in sockeye salmon.

Examination of data from chum salmon scale counts (Table 1), by sample location and sex, indicated some disparity among samples within these categories. Mean differences between left and right side counts of males were significant in one sample from the high seas. In this sample, collected by the MV "Paragon," the mean difference for females was not significant. In the Hokkaido Island sample both males and females

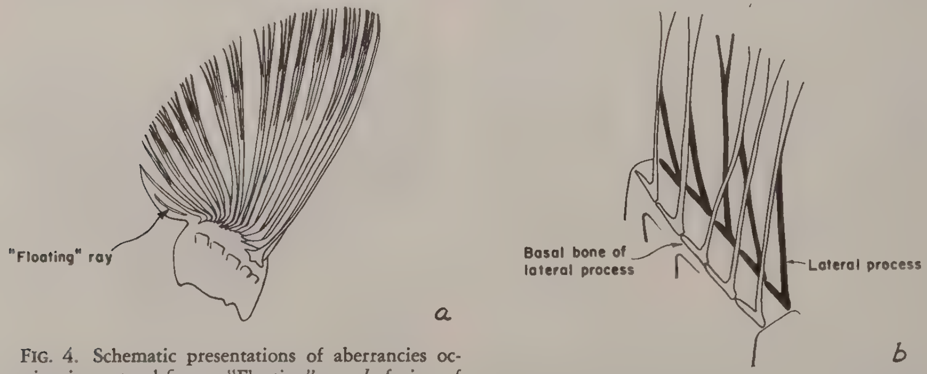

FIG. 4. Schematic presentations of aberrancies occurring in pectoral fins. *a,* "Floating" ray; *b,* fusion of lateral processes from adjacent fin ray bases.

TABLE 1

BILATERAL VARIATION IN THE NUMBER OF LATERAL LINE SCALES

SAMPLE SOURCE (YEAR)	SPECIES	SEX	NUMBER EXAMINED	% ASYMMETRICAL	% ASYMMETRICAL TOWARD LEFT	MEAN OF (L–R)	100 (P)
MV "Attu" 56°N, 173°W (1957)	sockeye	male	13	69.2	66.7	0.307	>50
		female	38	65.8	56.0	0.053	>50
		total	51	66.6	58.8	0.118	>50
53°N, 165°W (1957)	sockeye	male	32	68.8	50.0	–0.031	>50
		female	19	63.2	33.3	–0.579	>50
		total	51	66.6	42.8	–0.235	>50
50°N, 170° W (1957)	sockeye	male	11	72.7	37.5	0	—
		female	24	62.5	66.5	0.208	>40
		total	35	65.7	56.5	0.142	>50
Okanogan River (1957)	sockeye	male	11	90.9	50.0	0	—
		female	13	76.9	50.0	0.154	>50
		total	24	83.3	50.0	0.083	>50
Japanese Fishery 50°N, 168°E (1958)	sockeye	male	61	59.0	41.6	–0.197	>10
		female	54	68.5	43.2	–0.241	>10
		total	115	63.4	42.4	–0.217	> 5
51°N, 172°E (1958)	sockeye	male	49	75.6	44.1	–0.244	>10
		female	74	62.2	43.4	–0.175	>10
		total	119	67.2	43.7	–0.202	>10
Combined sockeye samples		male	173	68.8	46.2	–0.116	>10
		female	222	65.3	47.6	–0.126	>10
		total	395	66.8	47.0	–0.122	> 5
MV "Pioneer" 50°–53°N, 175°–180°W (1957)	chum	male	41	75.6	41.9	–0.341	>10
		female	33	72.7	20.8	–1.121	< 1
		total	74	74.3	32.7	–0.689	< 1
MV "Paragon" 50°–60°N, 175°W (1957)	chum	male	72	76.3	36.3	–0.430	< 5
		female	63	84.1	52.8	0.111	>50
		total	135	80.0	44.4	–0.178	>10
Hokkaido I. (1958)	chum	male	109	70.6	25.9	–0.670	< 1
		female	51	72.5	35.1	–0.608	< 2
		total	160	71.2	28.9	–0.650	< 1
Combined chum samples		male	222	73.4	32.5	–0.532	< 1
		female	147	77.6	40.4	–0.415	< 2
		total	369	75.1	35.7	–0.485	< 1

showed significant differences in counts from opposite sides. Approximately 78% of the total female chum salmon samples exhibited asymmetrical development, while only 73% of the males were asymmetrical. However, the probability levels for the mean differences between sides for both males and females were not significant. Scale counts from the combined total of 369 chum salmon indicated some asymmetrical development in 75% of the specimens. Of all the specimens with asymmetries, counts from the right sides exceeded the left in approximately 64%. The over-all mean difference between left and right side counts (–0.485) was significant at the 0.01 level.

Bilateral Variation in Gill Rakers

Gill raker counts from the first left and right branchial arches were collected from sockeye salmon taken at 10 locations (Table 2). Male and female groups varied similarly, with no significant values occurring in either category in the individual samples. Probability values for sexes combined were significant in samples from 3 locations. Bilateral asymmetry occurred in approximately 63% of the total of 668 sock-

TABLE 2

BILATERAL VARIATION IN THE NUMBER OF GILL RAKERS

SAMPLE SOURCE (YEAR)	SPECIES	SEX	NUMBER EXAMINED	% ASYMMETRICAL	% ASYMMETRICAL TOWARD LEFT	MEAN OF (L–R)	100 (P)
Nichiro	sockeye	male	70	58.6	58.5	.228	>10
50°–53°N,		female	93	63.4	59.3	.172	>10
160°–178°E (1956)		total	163	61.3	59.0	.196	< 5
Karluk River	sockeye	male	35	68.6	66.6	.343	> 5
(1957)		female	15	46.7	71.4	.200	>40
		total	50	62.0	67.7	.300	> 5
Naknek River	sockeye	male	12	66.7	75.0	.500	>10
(1957)		female	12	66.7	75.0	.583	> 5
		total	24	66.7	75.0	.542	< 5
Egegik River	sockeye	male	18	55.6	40.0	–.056	>50
(1957)		female	23	65.2	60.0	.130	>40
		total	41	60.9	52.0	.049	>50
Kvichak River	sockeye	male	12	75.0	66.6	.250	>20
(1957)		female	18	50.0	66.6	.278	>20
		total	30	60.0	66.6	.268	>10
MV "Tordenskjold"	sockeye	male	31	67.7	47.6	–.194	>10
51°N, 170°W		female	41	70.7	44.8	–.146	>10
(1959)		total	72	69.4	46.0	–.167	>10
52°N, 172°W	sockeye	male	17	88.2	66.7	.530	>10
(1959)		female	10	60.0	33.3	–.200	>50
		total	27	77.8	57.1	.259	>10
56°N, 170° W	sockeye	male	51	66.7	50.0	–.059	>40
(1959)		female	42	66.7	64.3	.333	>10
		total	93	66.7	56.4	.118	>10
51°N, 180°W	sockeye	male	22	59.1	61.5	.454	>10
(1959)		female	15	46.7	85.7	.533	> 5
		total	37	54.1	70.0	.486	< 5
USSR: Ozernaya River	sockeye	male	46	56.5	57.7	.174	>10
(1959)		female	85	60.0	51.0	0	—
		total	131	58.8	53.2	.061	>50
Combined sockeye		male	314	64.0	57.7	.172	< 1
samples		female	354	61.9	57.5	.136	< 5
		total	668	62.9	57.6	.153	< 1
MV "Celtic"	chum	male	41	46.3	21.1	–.366	< 1
50°–57°N,		female	29	62.1	44.4	–.172	>10
145°–154°W (1956)		total	70	52.8	32.4	–.286	< 1
Ketchikan	chum	male	11	27.3	33.3	–.090	>50
(1959)		female	9	77.8	71.4	.333	>10
		total	20	33.0	60.0	.100	>50
USSR: Ozernaya River	chum	male	63	61.9	43.6	–.111	>40
(1959)		female	39	51.3	45.0	–.027	>50
		total	102	57.8	44.1	–.078	>40
Bolshaya River	chum	male	22	63.6	50.0	.045	>50
(1959)		female	67	58.2	51.3	.015	>50
		total	89	59.6	50.9	.022	>50
Okhotsk River	chum	male	29	44.8	61.5	0	—
(1959)		female	42	47.6	40.0	–.119	>30
		total	71	46.5	48.5	–.070	>30

TABLE 2 (continued)

Combined chum samples		male	166	53.0	42.0	–.138	> 5
		female	186	55.9	48.1	–.038	>50
		total	352	54.5	45.3	–.085	> 5
Petersburg (1959)	pink	male	37	54.0	60.0	.027	>50
		female	18	72.2	61.5	.111	>50
		total	55	60.0	66.6	.054	>50
Fraser River (1959)	pink	male	31	64.5	60.0	.064	>50
		female	18	50.0	55.6	.056	>50
		total	49	59.2	58.6	.061	>50
Combined pink samples		male	68	58.8	60.0	.044	>50
		female	36	61.1	59.1	.083	>50
		total	104	59.6	59.7	.058	>50

eye salmon examined. Of specimens exhibiting asymmetry, 58% had larger left side counts. In the combined data for the species, left side counts exceed the right by 0.15 rakers, which was significant at the 0.01 level.

In chum salmon (Table 2), the mean differences between left and right side gill raker counts were significant for only one sample collected on the high seas in 1956. Mean differences and probability levels varied among the samples of both males and females, with no apparent evidence of sexual dimorphism. The probability level for the mean differences calculated for all males combined was greater than 5%, and for all females was greater than 50%. Of the total of 352 pairs of chum salmon gill raker counts, 54% showed asymmetrical development of the structures. Asymmetry was toward the right side, which averaged 0.085 more rakers in these specimens; however, this difference was not significant.

In pink salmon (Table 2), differences between left and right side gill raker counts varied little among the categories of sample location or sex. In this species, 59% of the males and 61% of the females examined showed some asymmetry in gill raker counts from opposite sides of the fish, with a slight but consistent tendency for the left side to exceed the right. The probability levels for the samples and for all specimens combined, however, indicated that the observed mean differences were not statistically significant.

Bilateral Variations in Branchiostegal Rays

Pairs of branchiostegal ray counts were collected from 407 sockeye, 350 chum, and 59 pink salmon (Table 3). Although very few specimens of pink salmon were examined, in this species, as well as in the other two, the females exhibited a greater percentage of asymmetrical development, with larger mean differences than the males. Only in sockeye samples from the Karluk and Egegik rivers, and in one chum salmon sample taken by the MV "Celtic," was the trend reversed. The mean differences observed were significant for all individual samples and also for each sample of male or female fish. In the combined data for each of the three species, asymmetrical development occurred in 62%, 77%, and 71% of the sockeye, chum, and pink salmon, respectively. Left side counts exceeded right side counts in 93% of the asymmetrical pairs of sockeye salmon branchiostegals, in 96% of the chums, and in 98% of the pink salmon. In sockeye salmon, the number of branchiostegal rays in the left side structures exceeded the right by approximately 0.6 rays; in chum and pink salmon the mean differences averaged 0.8 rays. The mean differences in all three species were statistically significant.

Bilateral Variation in Pectoral Fin Rays

Comparisons were made of fin ray counts from left and right pectoral fins of 407 sockeye, 357 chum, and 97 pink salmon (Table 4). No consistent trends were observed toward sexual dimorphism or effect of sampling location in respect to asymmetry of this character. For the combined data for each species, asymmetry occurred in only 14–24% of the specimens—much less frequently than for the other three characters examined. Variations in the number of rays from opposite sides resulted in very

TABLE 3

BILATERAL VARIATION IN THE NUMBER OF BRANCHIOSTEGAL RAYS

SAMPLE SOURCE (YEAR)	SPECIES	SEX	NUMBER EXAMINED	% ASYMMETRICAL	% ASYMMETRICAL TOWARD LEFT	MEAN OF (L–R)	100 (P)
Nichiro 50°–53°N, 160°–178°E (1956)	sockeye	male	41	61.0	80.0	.415	< 1
		female	72	54.2	87.0	.472	< 1
		total	113	56.6	84.0	.451	< 1
Karluk River (1957)	sockeye	male	35	60.0	90.0	.543	< 1
		female	15	46.7	100.0	.533	< 1
		total	50	56.0	89.0	.540	< 1
Naknek River (1957)	sockeye	male	14	64.3	100.0	.857	< 1
		female	18	77.8	100.0	.889	< 1
		total	32	71.9	100.0	.875	< 1
Egegik River (1957)	sockeye	male	22	81.8	94.0	.818	< 1
		female	24	70.8	100.0	.750	< 1
		total	46	76.1	97.0	.783	< 1
Kvichak River (1957)	sockeye	male	13	38.5	100.0	.385	< 5
		female	16	87.5	100.0	.938	< 1
		total	29	65.5	100.0	.690	< 1
Ozernaya River (1959)	sockeye	male	46	52.2	95.8	.522	< 1
		female	91	65.9	95.0	.659	< 1
		total	137	61.3	95.2	.613	< 1
Combined sockeye samples		male	171	59.6	91.2	.556	< 1
		female	236	64.0	94.7	.640	< 1
		total	407	62.2	93.3	.604	< 1
MV "Celtic" 50°–57°N, 145°–154° W (1956)	chum	male	39	76.9	73.6	.820	< 1
		female	31	80.6	96.0	.774	< 1
		total	70	78.6	94.5	.800	< 1
Ketchikan (1959)	chum	male	13	76.9	100.0	.923	< 1
		female	9	77.8	100.0	1.333	< 1
		total	22	77.2	100.0	1.090	< 1
Ozernaya River (1959)	chum	male	58	75.9	90.9	.655	< 1
		female	39	92.3	100.0	.974	< 1
		total	97	82.5	95.0	.784	< 1
Bolshaya River (1959)	chum	male	24	70.8	88.2	.625	< 1
		female	67	77.6	100.0	.900	< 1
		total	91	75.8	97.1	.824	< 1
Okhotsk River (1959)	chum	male	29	62.1	94.4	.552	< 1
		female	41	73.2	100.0	.854	< 1
		total	70	68.6	97.9	.728	< 1
Combined chum samples		male	163	73.0	92.4	.693	< 1
		female	187	80.2	99.3	.904	< 1
		total	350	76.8	96.3	.806	< 1
Ketchikan (1959)	pink	male	31	67.7	95.2	.677	< 1
		female	28	75.0	100.0	.893	< 1
		total	59	71.2	97.6	.780	< 1

TABLE 4

BILATERAL VARIATION IN THE NUMBER OF PECTORAL FIN RAYS

SAMPLE SOURCE (YEAR)	SPECIES	SEX	NUMBER EXAMINED	% ASYMMETRICAL	% ASYMMETRICAL TOWARD LEFT	MEAN OF (L–R)	100 (P)
Nichiro 50°–53°N, 160°–178°E (1956)	sockeye	male	40	25.0	60.0	.075	>40
		female	69	21.7	53.3	.014	>50
		total	109	22.9	56.0	.037	>40
Karluk River (1957)	sockeye	male	36	19.4	57.1	.028	>50
		female	16	31.2	40.0	–.062	>50
		total	52	23.0	50.0	0	—
Naknek River (1957)	sockeye	male	14	42.8	16.6	–.286	>10
		female	17	29.4	60.0	.059	>50
		total	31	35.4	36.3	–.097	>20
Egegik River (1957)	sockeye	male	22	22.7	40.0	–.045	>50
		female	23	13.0	66.7	.043	>50
		total	45	17.7	50.0	0	—
Kvichak River (1957)	sockeye	male	13	15.3	50.0	0	—
		female	18	16.6	33.3	–.056	>50
		total	31	16.1	40.0	–.032	>50
Ozernaya River (1959)	sockeye	male	47	17.0	75.0	.085	>10
		female	92	22.8	57.1	.022	>30
		total	139	20.9	62.1	.058	>20
Combined sockeye samples		male	172	22.1	52.6	.017	>50
		female	235	22.1	53.8	.021	>40
		total	407	22.1	53.3	.019	>40
MV "Celtic" 50°–57°N, 145°–154°W (1956)	chum	male	41	31.7	46.1	–.024	>50
		female	31	29.0	44.4	–.032	>50
		total	72	30.5	45.4	–.027	>50
Ketchikan (1959)	chum	male	13	23.0	66.7	.076	>50
		female	10	40.0	75.0	.200	>10
		total	23	30.4	71.4	.130	>10
Ozernaya River (1959)	chum	male	62	19.4	41.6	–.032	>50
		female	38	15.8	83.3	.105	>10
		total	100	18.0	55.6	.020	>50
Bolshaya River (1959)	chum	male	23	13.0	66.7	.043	>50
		female	68	23.5	75.0	.118	>20
		total	91	20.9	73.7	.099	>20
Okhotsk River (1959)	chum	male	29	10.3	66.7	.034	>50
		female	42	16.7	57.1	.024	>40
		total	71	14.1	60.0	.028	>50
Combined chum samples		male	168	23.8	50.0	–.006	>50
		female	189	22.2	66.7	.074	>50
		total	357	21.3	59.2	.036	>50
Ketchikan (1959)	pink	male	38	13.2	60.0	.026	>50
		female	12	16.7	100.0	.166	>20
		total	50	14.0	71.4	.060	>20
Prince William Sound (1959)	pink	male	40	15.0	66.7	.050	>50
		female	7	42.8	00.0	–.428	>10
		total	47	19.1	44.4	–.021	>50
Combined pink samples		male	78	14.1	63.6	.042	>10
		female	19	26.3	40.0	–.053	>50
		total	97	16.5	56.2	.021	>50

small mean differences for all three species; the mean differences for sockeye and pink salmon were approximately 0.02 and for chums 0.04. Although the left pectoral fin counts generally exceeded the right, the tests for differences were not statistically significant for any sample or species.

CONCLUSIONS

The results of this study show that sockeye, chum, and pink salmon, which are essentially bilaterally symmetrical animals, exhibit some asymmetries with respect to all four paired meristic characters considered. From the specimens examined no conclusive relationship was shown between the occurrences of asymmetries and the sex or the area from which samples were obtained; however, these possible sources of variation were not rigidly tested, for reasons given earlier in the text.

In taxonomic and racial studies involving lateral line scale counts, interchanging counts from left and right sides of chum salmon introduces an additional source of variation and, in a situation of considerable numbers of substitutions, may be a serious source of bias. In sockeye salmon, substitution of one side for another appears feasible; however, variation in the probability levels of individual samples suggests that, for more complete assurance of reliability, examination of a larger number of sockeye salmon specimens would be desirable.

Substitution of gill raker counts from sockeye salmon is not advisable. In chum salmon the observed differences in left and right side counts are not statistically significant; however, the differences observed in one high seas sample containing 70 specimens raise some doubt in situations in which loss of a character, resulting in reduced sample size, is a lesser problem than maintaining minimum variations in the data to be collected. Gill raker counts from opposite sides of pink salmon vary equally, and substitution of the opposing structure will not seriously affect the analysis.

In the species considered, branchiostegal counts from left and right sides can not be reliably interchanged. Also, the extent of the asymmetry observed in this character is of a greater magnitude in female salmon. Further study of sexual differences in left and right side variations is required, however, to yield conclusive evidence of the existence of sexual dimorphism in respect to bilateral variations in branchiostegals of Pacific salmon.

Pectoral fin rays from the left and right side structures are essentially equal in number in all three species. Substitution of sides in obtaining counts of pectoral fin rays would contribute little variation to mean counts of this character.

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Feeding, Growth, Respiration, and Carbon Utilization of a Euphausiid Crustacean[1]

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ABSTRACT

In the euphausiid shrimp *Euphausia pacifica*, a member of the oceanic plankton, growth was as rapid as 0.048 mm/day in juveniles in the laboratory, more than twice as fast as that observed for oceanic populations (0.02 mm/day) by other workers. Periods between molting, which occurs throughout the life span, varied between 3 and 8 days depending on the temperature but not on the amount of food eaten. Respiration accounted for the major portion of the assimilation of carbon (62–87%) and molting, growth, and reproduction accounted for the remainder. In mature animals, 9% of the assimilated carbon was released as the organic portion of the eggs. Rapidly growing animals incorporated as much as 30% of the assimilated carbon, but calculations for an oceanic population gave 9% as the incorporation of organic carbon into tissue (excluding eggs and molts) over the life span of the animal. Assimilation of ingested carbon (digestion) appeared to be high, usually over 80%, as judged from tracer experiments. In the laboratory, crustacean nauplii seemed to be a preferred food over unicellular algae but both were eaten when available; one alga was rejected. Nauplii must be smaller than 0.8 mm for many to be ingested by adult *E. pacifica*. Molting, which mainly occurred at night, depressed feeding. The filtering rates for the animal on unicellular algae are sufficient for growth and metabolism if the carbon available to the animal in the sea is equivalent to that contributed by both detritus and phytoplankton standing crop in the area of the northeastern Pacific Ocean where *E. pacifica* is found. It is suggested that adult *E. pacifica* must capture between 100 and 200 nauplii per day as 1-year-olds and 200–300 per day as 2-year-olds to satisfy all of its carbon requirements. The mean density of small crustaceans in nature is probably too low for this animal to fulfill its needs. However, concentrations may be high enough in local aggregations.

INTRODUCTION

THIS PAPER reports on an experimental study of the euphausiid crustacean *E. pacifica* and describes in quantitative terms its growth, molting, feeding, respiration, and the efficiency with which it incorporates carbon from its food into body tissue. The information obtained in the laboratory is compared wherever possible with observations made by others on the same species in nature.

Ultimately the marine scientist wishes to be able to predict the yield of fish flesh in the ocean through knowledge of primary production by the standing crop of phytoplankton. Without quantitative information on the efficiency with which organic carbon is transferred from one trophic level to another, no predictions of this kind are possible.

Measurements of organic carbon production by phytoplankton are now made routinely in all the oceans of the world (U.S. Atomic Energy Comm., 1961), but few studies have been made on the utilization of this carbon by zooplankton. In recent years, following the pioneering work of Marshall and Orr (1955) on the copepod *Calanus finmarchicus*, some of the numerically more important planktonic animals, chiefly copepods, have been studied experimentally in the laboratory (see review by Conover, 1964).

Among the planktonic organisms in the food web of the oceans, the euphausiid crustaceans rank high in abundance and importance. They are food for a variety of fishes ranging from albacore (McHugh, 1952) to salmon (Merkel, 1957) and sardines (Hand and Berner, 1959) and are the chief food of baleen whales (Marr, 1962). Euphausiids may also contribute substantially to the detritus of the ocean because they molt regularly and frequently throughout their life (Lasker, 1964; Jerde and Lasker, 1966). An intimate knowledge of the physiology of euphausiids is essential before their potential and actual *in situ* ability to capture food and incorporate carbon can be known.

Euphausia pacifica Hansen, the most abundant euphausiid off the California coast, has been shown by Brinton (1962) to be an important indicator of oceanic water masses in the northern Pacific Ocean. Ponomareva (1954, 1955, 1959, 1963), among others, has investigated the ecology of this species and has analyzed information on feeding habits, growth, and fecundity from field collections. Osterberg et al. (1964) found this species to be an indicator of radioactivity contamination off the west coast of the United States and an important component of the food web of the northern Pacific Ocean. Boden et al. (1955) in an excellent monograph offer extensive discussion of the distribution of this and other euphausiids of the Pacific Ocean.

MATERIALS AND METHODS

Methods for the collection and maintenance of euphausiids in the laboratory were described by Lasker and Theilacker (1965). These techniques were used to capture and to maintain *E. pacifica* in the laboratory over 1 year at temperatures ranging from 6.5 to 16 C. *Euphausia pacifica* grows steadily and molts regularly on a diet of newly hatched *Artemia salina* nauplii. Euphausiids grow throughout their life and the uropods of the molts show successive increments in length which are proportional to the increase in "body length" which (Fig. 1) is in turn related to dry weight. "Body length" was measured as the length of the carapace from behind the eye to the junction of the abdomen and telson in straight animals. The relations between uropod length and body length (Fig. 2) allow the estimation of dry weight at any stage of growth by measurement of the uropod length at molting. Live animals were measured after being anesthetized in isotonic $MgCl_2$; after a rinse in distilled water, they were dried to a constant weight over silica gel in an oven at 50–60 C and weighed. Formalin-preserved animals could not be used because they have a different length:weight relationship; the weight for a

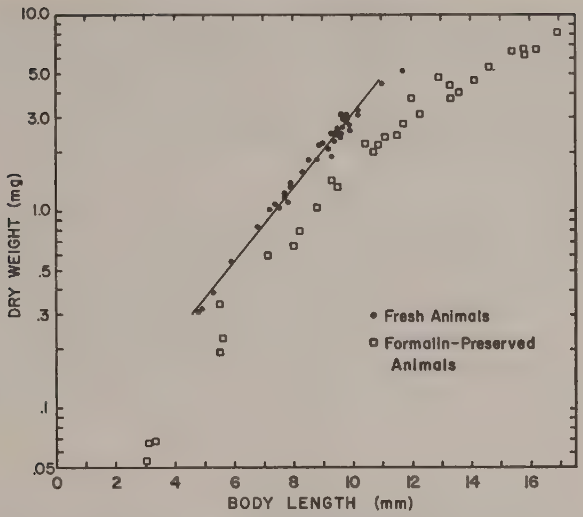

FIG. 1. Relation between body length and dry weight for fresh and formalin-preserved *E. pacifica*.

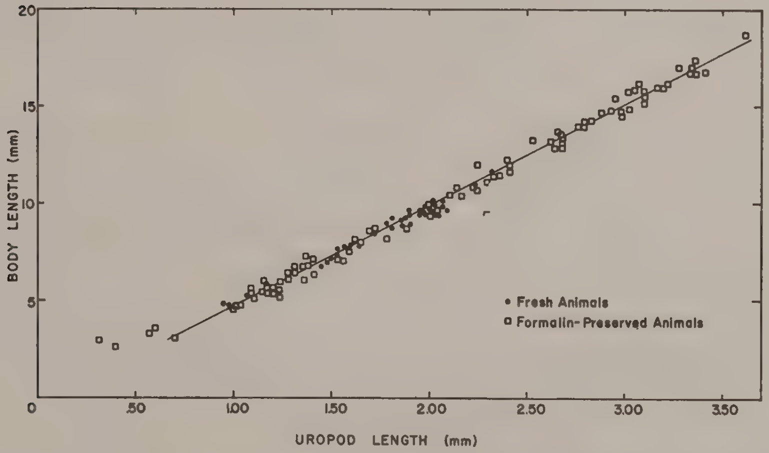

FIG. 2. Relation of body length (measured from behind the eye to the junction of the telson) to uropod length for fresh and formalin-preserved *E. pacifica*.

given length is considerably less than that of fresh animals (Fig. 1). Loss of body weight due to formalin preservation was further indicated by the low quantity of ash, 3.5% of dry weight, found in preserved euphausiids as compared to 10.5% of dry weight in fresh animals. The remainder of the loss is undoubtedly due to leaching of organic materials.

Each animal used in a growth experiment was observed daily, the temperature of the water was recorded, and molts were removed if present. The molt uropods were measured, the molt was rinsed once in distilled water and dried on a microscope slide for subsequent weighing with a Cahn electrobalance to ±0.002 mg. Some molts were preserved in 3% buffered formalin for uropod measurement only. Both uropods were examined in every case because occasionally one of them was damaged; when this occurred only the undamaged one was measured.

In experiments where carbon-14 was used, the technique was modified from Lasker (1960). In each experiment, 20–30 μc of carbon-14 were added as $NaHC^{14}O_3$ prepared by the method of Steemann-Nielsen (1952). The $NaHC^{14}O_3$ was inoculated into 60 ml of a dense suspension of a bacteria-free culture of a unicellular green alga, *Dunaliella primolecta*, *D. tertiolecta*, or *Platymonas subcordiformis*. After incubation under a fluorescent light for more than 24 hr, the algae were fed to *Artemia salina* nauplii which had just begun to feed. Feeding was allowed to continue 24 hr at room temperature after which the nauplii were collected on netting, rinsed in sea water, and transferred to a medium containing nonradioactive algae. Feeding on the nonradioactive algae for 20 hr caused the nauplii to clear their guts of undigested radioactive algae. At the temperature at which the experiments with the euphausiid were performed (ca. 10 C), *Artemia* nauplii respire and grow very slowly. For short-term experiments (of 1 day or less) the amount of carbon in the *Artemia* nauplii changed imperceptibly and the ratio of carbon-14 to total carbon was not altered. The calculations of carbon-incorporation efficiency were the same as those described by Lasker (1960).

All carbon-14 measurements were made with a Nuclear Chicago vibrating-reed electrometer (Dynacon) after wet combustion of the tissue to be analyzed to carbon dioxide (Van Slyke et al., 1951). This procedure obviated the problems usually encountered with Geiger counting such as self-absorption, back scattering, and variable geometry. Total carbon in animal and plant tissue was measured with an F and M carbon analyzer model 180. The method is based on a dry combustion at 800 C in the presence of an oxidizing agent (Ag_2O) and the subsequent separation of gaseous combustion products with a gas chromatograph. A lower limit of 100 μg of carbon can be detected with this apparatus to ± 1% precision.

Euphausiids and their molts were analyzed for total nitrogen by the standard Kjeldahl method. Ash was determined by combusting whole animals or molts at 500–525 C and weighing the residue.

Experiments on filtering rate were done by supplying *E. pacifica* with a known number of algal cells and by counting the cells remaining after a suitable interval of feeding time, usually 24 hr. Algal cells were counted with a Coulter Counter Model A. Calculations of milliliters cleared per unit time, or filtering rate (F), were made from the formula derived by Gauld (1951),

$$F = V \frac{(\log_{10} C_0 - \log_{10} C_t)}{(t \log_{10} e)}$$

where C_t is the concentration of cells at time t, C_0 the initial concentration, and V the volume. Corrections for increases in cell number due to cell divisions were made by reference to a control.

When *Artemia* nauplii were supplied as food, the actual number of nauplii was determined before and after the feeding to determine a filtering rate, or more properly, a capture rate. Experiments were done in the dark to assure the random distribution of nauplii in the experimental container.

Respiration was determined by standard Warburg manometry after acclimation of euphausiids to the testing temperature (usually 10 C) for more than 12 hr. In order not to disturb the animals excessively, the manometers were shaken 5 min each half hour at 60 cycles/min to establish gaseous equilibrium. Q_{O_2} (oxygen consumed) is reported here as microliters of O_2/milligram dry weight per hour.

GROWTH

Ecdysis is important in the physiology of euphausiids because growth, as in all arthropods, is accompanied by molting. Unlike copepods, however, euphausiids continue to grow throughout their life span. In an earlier paper Lasker (1964) observed that *E. pacifica* molts on the average every 5 days at temperatures similar to those at which the animal lives in the sea (ca. 9–15 C). Other euphausiid species from neritic as well as oceanic habitats are known to molt at about the same frequency in laboratory containers (Jerde and Lasker, 1966).

Temperature was found to be an important exogenous factor regulating molting in *E. pacifica*. For a large number of *E. pacifica* ranging from 1 to 9 mg dry weight at the daily temperatures of the refrigerated sea water supplied in the Scripps Institution of Oceanography's experimental aquarium, the euphausiid's intermolt periods varied as the water temperature fluctuated (Fig. 3). For a single organism the intermolt period was shortened rapidly by an artificially produced warm period (Fig. 4). Three days seemed to be the minimum intermolt period (maximum molting rate); temperatures above 12 C did not accelerate molting further. Over a 3½ month period at elevated temperatures near 15 C, 12 *E. pacifica* shed a total of 83 molts. Of these molts, 6% were spaced at 5 days; 53% at 4 days; 37% at 3 days; 3% at 2 days, and 1% at 1 day.

Each cast skin represents loss of a sizable quantity of organic material by the animal. Lasker (1964) pointed out that the dry weight of each molt is approximately 10% of the dry weight of the *E. pacifica* which produced it. This figure is also close to the average molt weight for six other species of euphausiids reported by Jerde and Lasker (1966). Dry weight of the molt from a single animal may vary from 4 to 14% of the animal's dry weight. Molts contained approximately 46% ash, 17% organic carbon, and 2.5% organic nitrogen (Table I). No inorganic carbon was detectable, therefore, about 4% of a euphausiid's carbon and 2% of its nitrogen may be lost at each ecdysis.

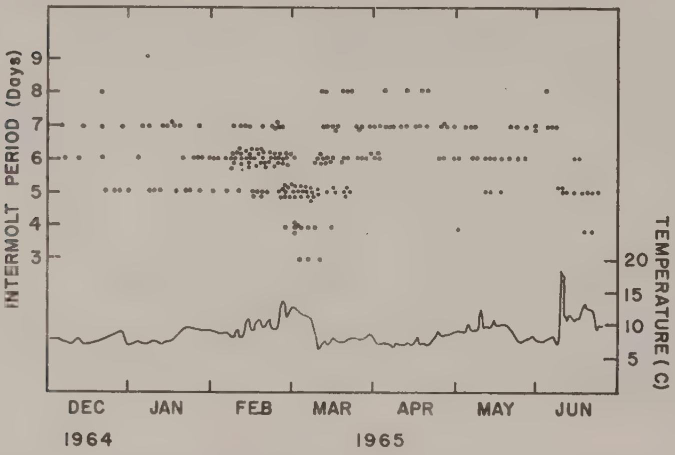

FIG. 3. Intermolt periods for individual *E. pacifica* in relation to the temperature of the laboratory sea water. Each dot represents one animal's intermolt period at the temperature indicated by the curve below. Additional animals caught in February 1965 account for the large number of dots in February and March.

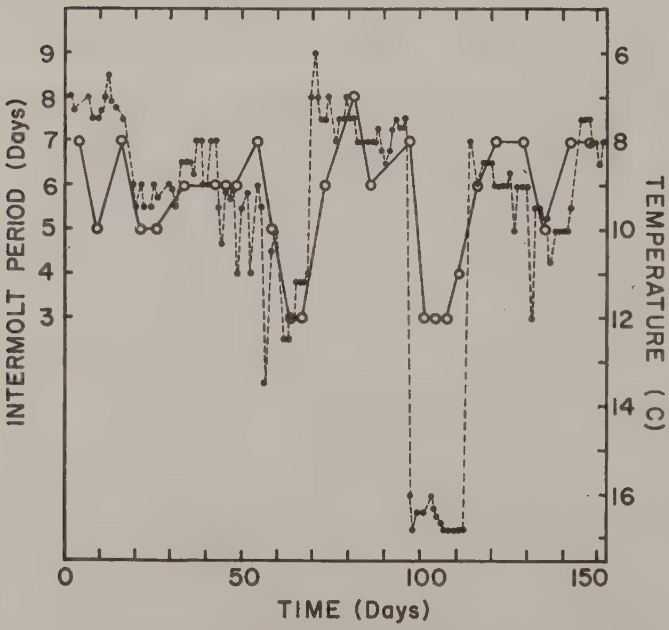

FIG. 4. Intermolt periods of a single *E. pacifica* in relation to temperature. To ascertain the effect of a change in temperature on molting, the sea water was intentionally warmed between the 97th and 112th days. Temperature is indicated by the broken line and closed dots; molting frequency is shown as open dots connected with a solid line.

TABLE I. Per cent chemical composition of *E. pacifica* and molts.

Item	*E. Pacifica*		Molts[a]
	Mean	Range	
Water	82.8±3.8 (9)[b]	78.7–89.6	
Dry weight (by difference)	17.2		
Ash of dry weight	10.5 (5)	9.9–13.0	45.5
Carbon of dry weight	42.0±1.7 (22)	38.1–45.1	17.0
Nitrogen of dry weight	11.5 (5)	10.4–13.0	2.5

[a] Molts were pooled for analysis.
[b] Mean, standard deviation, and number of replicates.

INCREASE IN LENGTH

Growth in length as determined from measurements of molt uropods is illustrated in Fig. 5 and 6 for seven experimental animals supplied with a surplus of *Artemia* nauplii as food in 1-liter containers of sea water kept in the dark at 10 C. The three animals whose growth curves appear in Fig. 5 were observed soon after the furcilia stage of development as juveniles, i.e. each had developed a single terminal spine and had only two pairs of postero-lateral spines as described by Boden (1950). These euphausiids showed a steady linear growth and almost equally spaced molts. In the smallest animals,

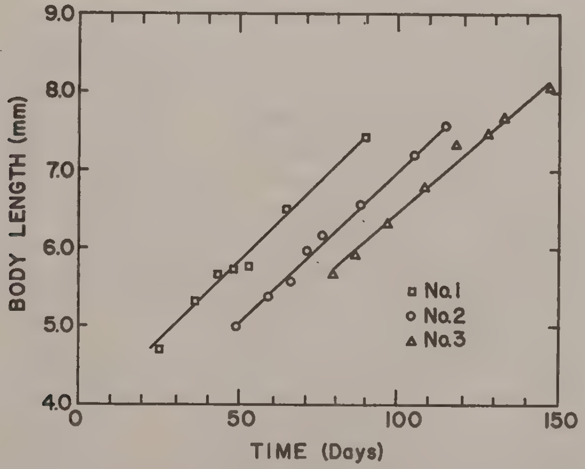

FIG. 5. Growth in length of three juvenile *E. pacifica* maintained in the laboratory at approximately 10 C. Gain in weight for these same animals is depicted in Fig. 7.

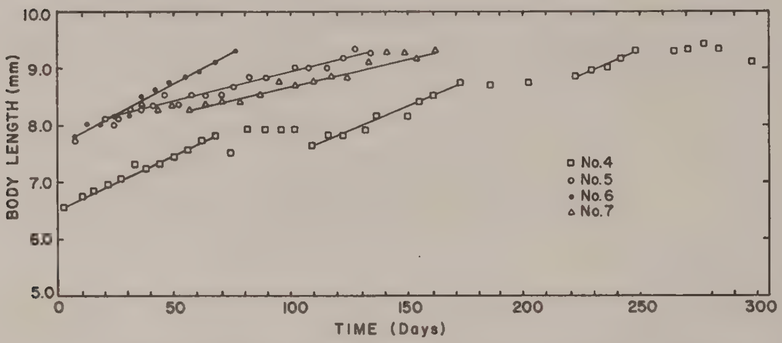

FIG. 6. Growth in length of four adult *E. pacifica* maintained in the laboratory at approximately 10 C. Gain in weight for these animals is depicted in Fig. 8.

No. 1 and 2 (Fig. 5), the lengths and dry weights were similar — 4.72 mm and 0.28 mg in animal No. 1, 4.95 mm and 0.30 mg in animal No. 2. Animal No. 3 was 5.65 mm and 0.50 mg at the beginning of the study of linear growth. The initial lengths of other animals in the growth experiments varied from 6.3 to about 8.0 mm. The smallest animals had the fastest growth rates, 0.034–0.048 mm/day.

The laboratory-maintained animals included euphausiids which did not grow in spite of sufficient food. Molting of these animals continued uninterrupted but the animals became progressively shorter and died within a few weeks or months. These examples indicate that molting is a metabolic necessity and continues at the expense of the organic reserves of the animal.

Following the rapid growth period of animals 1, 2, and 3 (Fig. 5) they were kept about 1 month between 10.5 and 13.5 C due to a failure of the laboratory seawater cooling system. The growth, after a short lag period, decreased drastically (to 0.0016 mm/day). When the water was cooled and maintained once again below 10 C, the former growth rate resumed, again after a lag period of 1 month. Feeding may have been adversely affected and the extra metabolic demand due to warming probably was enough to reduce the carbon that ordinarily went into growth.

Ponomareva (1959, 1963) has observed that *E. pacifica* spawns only once a year, in midJune, in the northwest Pacific–Bering Sea, and that the furcilia stage is reached in 16–18 days after spawning. She distinguished two modal groups characterized by different lengths[2] in her winter collections and deduced that the euphausiid grows to 10 mm in 1 year and to 15 mm in 2 years. Sexual maturity is achieved in 1 year.

The most rapid rate in laboratory experiments over the length interval of 5–8 mm (0.048 mm/day) was more than twice the rate (0.019 mm/day) calculated from the information of Ponomareva. The favorable conditions for the laboratory animals, particularly the availability of food, may account for the faster growth.

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[2] The telson of *E. pacifica* is 20% of the total length. To make the figures of Ponomareva (1963) comparable to the body length measurements reported in this paper I have subtracted 20% from the total lengths reported by her.

Increase in Weight

Animals 1, 2, and 3 had similar growth in weight (Fig. 7) as well as in length, and it may be inferred that all three animals were feeding to their maximum on the excess number of *Artemia nauplii* that were supplied.

Animal No. 1 increased in dry weight 0.0139 mg/day for 65 days at 10 C and shed 11 molts. The molts weighed less than the average for *E. pacifica*: 6% as opposed to 10–11% (Lasker, 1964; Jerde and Lasker, 1966) of the dry body weight at each molt. Animal No. 2 gained 0.0142 mg/day. In 67 days 12 molts were shed and each averaged 4% of the dry body weight. Animal No. 3 gained 0.0146 mg/day for 68 days with each of 13 molts averaging 4% of the dry body weight.

For the four other animals the increases in weight ranged from 0.004 to 0.015 mg/day (Fig. 8).

Increase in mass of individual *E. pacifica* over a period of 20 months after hatching was calculated for the Bering Sea population from Ponomareva's (1963) data. The calculations were not extended beyond this period because

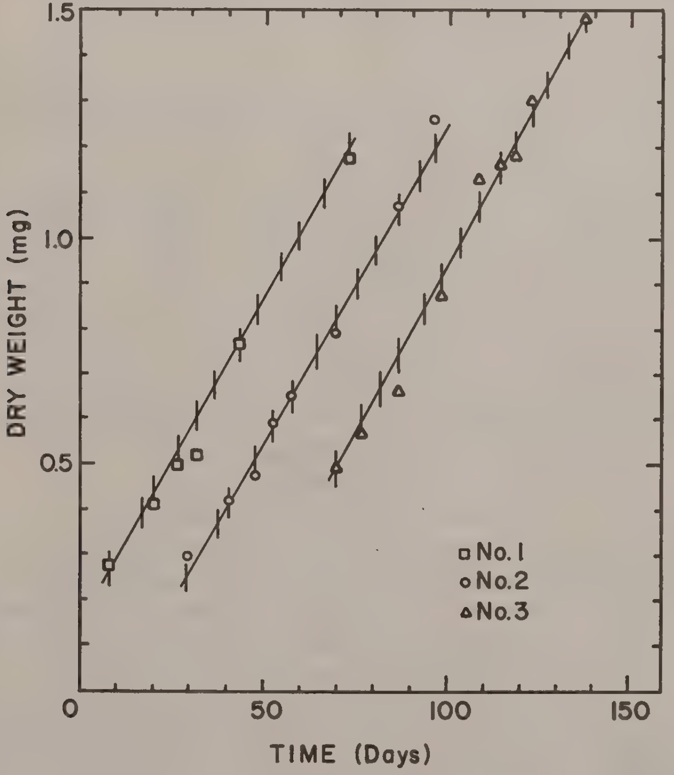

FIG. 7. Increase in dry weight of three juvenile *E. pacifica* maintained in the laboratory. Same animals as in Fig. 5. The vertical dashes indicate when molting occurred.

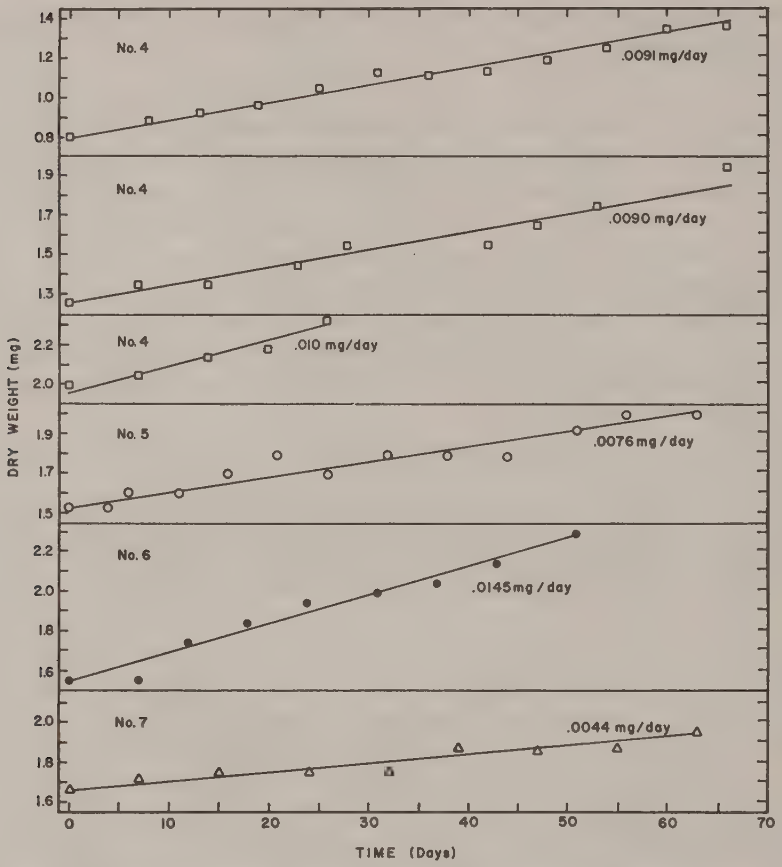

FIG. 8. Increase in weight of adult *E. pacifica* maintained in the laboratory. Same animals as in Fig. 6.

I lacked weight–length information for the larger individuals. *Euphausia pacifica* averaged 1 mg dry weight 7 months after hatching, 2.6 mg in 1 year, and 9 mg after 20 months.

RESPIRATION

The oxygen consumption of *E. pacifica* for young and old animals was determined. For animals with dry weights 1.05–9.65 mg held at 10 C (Fig. 9) the mean oxygen consumption (Q_{O_2}) was 1.47 μliter O_2 per mg dry weight per hr (standard deviation = ±0.35) and appeared to be independent of the size of the animal.[3] A vertical profile (Fig. 10) of the distribution of *E. pacifica* in the water column taken by Longhurst et al. (1966) in the San Diego area shows that during the daytime most are between 8 and 11 C. Clarke (1966)

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[3] Euphausiids move their swimming appendages rapidly and continually, presumably to aerate their external gills. Oxygen uptake remains the same whether or not an animal is swimming.

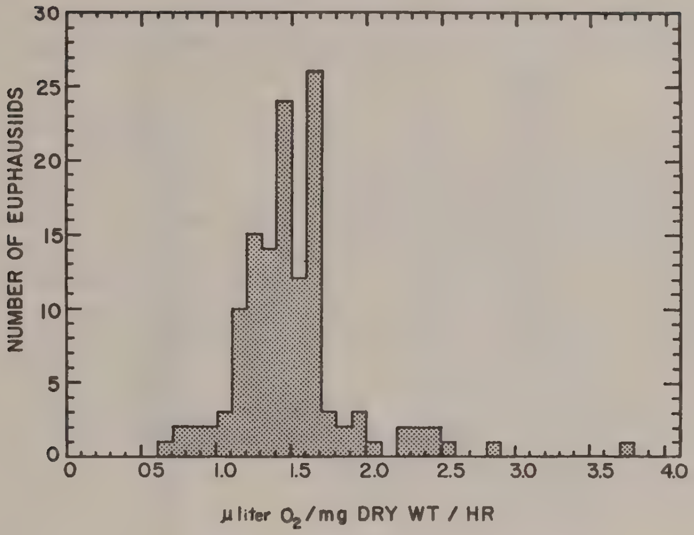

FIG. 9. Rate of oxygen consumption of 122 *E. pacifica* at 10 C. Dry weights ranged from 1.05 to 9.65 mg.

showed that this restricted distribution is due to a sharp self-confinement of the population to a specific light intensity (10^{-3} to 10^{-4} μw/cm^2) in the Santa Barbara Basin, which is northward of the San Diego Trough where I collected the euphausiids for this study. In 1965 Clarke (1966 and unpublished data) monitored the diurnal isolume situation for several days in each month, collected plankton at specific depths, and simultaneously recorded vertical temperature profiles. From the diurnal distribution of the isolumes I deduced the depth of the bulk of the *E. pacifica* population and the time spent at any specific temperature during representative days of each month. The detailed data will be published elsewhere by Dr Clarke and his associates[4] but he has kindly consented for me to use his data to calculate the average temperature for the *E. pacifica* population over the entire year. During daylight hours, regardless of the month, *E. pacifica* resides in 8–10 C water and rises rapidly into surface waters at dusk. The overall average temperature at which the bulk of the population resided during 1965 was 11.05 C. My measurements of euphausiid respiration were made at 10 C and I have not introduced any correction factor owing to the small difference between the test and environmental temperatures in comparison with the normal variation in oxygen consumption.

EFFICIENCY OF CARBON UTILIZATION

Carbon incorporation efficiency, as used in this paper, is the percentage of the ingested carbon which appears in the tissue of the euphausiid during

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[4] General Motors Research Laboratories, Santa Barbara, California.

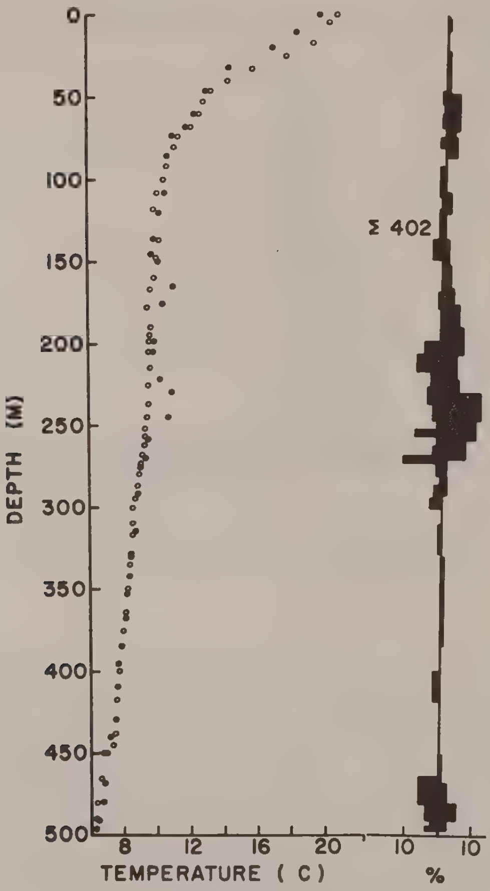

FIG. 10. Vertical distribution (percentages) of *E. pacifica* in the San Diego Trough, 32°42.7′N, 117°26.8′W, May 18, 1965, 1725 to 1815 local time, taken by Longhurst et al. (1966). Results for the descending plankton recorder are given on the left bar graph and the ascending on the right. The temperature profile shown at the far left was taken simultaneously.

short-term feeding experiments. It includes any carbon which may have been deposited in molts or reproductive products. This efficiency is analogous to the "gross growth efficiency" defined by Conover (1964) but with carbon substituted for weight or calories.

Assimilated carbon refers to the portion of ingested carbon which is digested by the euphausiid, and is analogous to Conover's "assimilation efficiency." The fraction of the assimilated carbon which appears in the tissues of the euphausiid due to growth is referred to as incorporation of assimilated carbon (Conover's "net growth efficiency") and can be distinguished from the remainder of the assimilated carbon, which is lost in molts, reproductive products, or respired carbon dioxide.

LABORATORY CARBON BUDGETS

From the percentage carbon determined for the dry weight of *E. pacifica* (42.0 ± 1.7%) the amount of organic carbon can be calculated for any size of individual. If increase in weight is known, therefore, the appropriate conversions yield information on the addition of organic carbon due to growth (carbon incorporation). Calculation of the carbon lost due to molting was based on actual molt weights obtained from laboratory animals and the amount of carbon that these molts contained. The loss of carbon due to molting in the field population was based on 10% weight loss every 5 days observed by Lasker (1964) and Jerde and Lasker (1966) and 17% organic carbon content of the molt. Respired carbon was calculated for *E. pacifica* during specific growth periods from the mean respiratory rate of 1.47 μliters O_2 per mg per hr and a respiratory quotient of 0.8 which assumes chiefly a fat and protein metabolism.

The carbon budgets for seven experimental animals (Table II) show that where growth is rapid incorporation of assimilated carbon is high and may account for as much as 30% of all the carbon entering the tissue of the animal. Where growth is slower, incorporation is as low as 6%. The long-term loss of carbon due to molting ranged from 6 to 11%; respiration accounted for 62–87% of the assimilated carbon.

Ponomareva (1963) stated that spawning of *E. pacifica* takes place in June in the Bering Sea and in the following winter two modal groups, presumably of successive year-classes, can be found at about 6.4 and 11.6 mm body length. In spring of the following year the two groups grow, respectively, to 10 and 15 mm body length. Using the weight–length relationship for fresh animals shown in Fig. 1, I converted Ponomareva's length figures to weight and calculated the carbon budget of the population (Table II), using laboratory data on molting and respiration. Because the respiratory need for carbon of the animal predominates over the life span, the incorporation of assimilated carbon is about 9%, not including eggs and molts.

Some information is available on reproduction of this euphausiid species. Ponomareva (1959) has counted the ova in *E. pacifica* from the northwest Pacific Ocean and has deduced that the fecundity is 1400 eggs. In a personal communication (1965) she has written me that spawning occurs only once in the life span of the species in the region of the Japan Sea, the Bering Sea, and the northwest Pacific Ocean. I obtained some *E. pacifica* eggs immediately after spawning. They weighed 5μg dry weight per egg, and contained about 50% C. A fecundity of 1400 eggs per female implies that 3.5 mg C were incorporated into ova during the life span of the female. The fraction of assimilated carbon calculated to appear in eggs was 9%. No information is yet available on the carbon needed by males for reproduction.

TABLE II. Weight and percentage incorporation of assimilated carbon by *E. pacifica*.

Animal No.	Initial dry weight (*mg*)	Final dry weight (*mg*)	Time (*days*)	Weight of assimilated carbon (*mg*)				Percentage of carbon incorporated			Percentage carbon used in respiration
				Growth	Molts	Respi-ration	Eggs	Growth	Molts	Eggs	
Laboratory animals											
1	0.30	1.19	69	0.37	0.10	0.78		30.0	8.0		62.0
2	0.30	1.20	73	0.39	0.07	0.83		29.6	5.7		64.7
3	0.50	1.50	69	0.42	0.11	1.04		26.8	6.8		66.4
4	1.56	2.30	51	0.31	0.15	1.49		15.9	7.7		76.4
5	0.80	1.36	66	0.24	0.094	1.08		16.7	6.6		76.7
	1.32	1.85	65	0.25	0.12	1.53		13.1	6.4		80.5
	1.95	2.31	23	0.15	0.066	0.84		14.3	6.2		79.5
6	1.53	2.00	63	0.20	0.24	1.68		9.4	11.3		79.3
7	1.65	1.94	63	0.12	0.14	1.71		6.2	7.0		86.8
Field population[a]											
	0.23	9.0	580	3.68	5.95	26.1	3.5	9.4	15.3	8.9	66.4

[a] Growth of field population based on data of Ponomareva (1963).

To summarize, over the 20 month span after hatching from the egg the average female *E. pacifica* in Ponomareva's study was calculated to respire 67% of its assimilated carbon and to invest 9% in growth, 15% in molting, and 9% in the production of eggs.

Experiments With Carbon-14

In earlier short-term experiments (24 hr) where *E. pacifica* were fed on unicellular algae, usually over 90% of the food was assimilated and the carbon incorporation efficiency ranged from 11 to 74% (average 32%) of the ingested carbon (Lasker, 1960). Because of their short-term nature these experiments included as "incorporated" any carbon which was mobilized into the molts of the animals and was destined to be descarded. The Q_{O_2} used then was 1.14 μliters per mg per hr, whereas a more reliable value obtained from many additional measurements, and the one used here is 1.47 μliters per mg per hr.

For *Artemia* nauplii to become sufficiently radioactive they must develop beyond the yolk stage and feed on suspended radioactive algae. Unfortunately, the *Artemia* have grown so large (to ca. 0.75 mm long) by the time they are sufficiently radioactive (5 days old) that *E. pacifica* has difficulty ingesting them. Consequently, almost all of the experiments (Table III) show assimilation of carbon from food which was not eaten in great enough quantity to meet all the metabolic needs of the animal. Four euphausiids (No. 8, 10, 13, and 14) ate enough or almost enough nauplii to satisfy their complete metabolic needs. Assimilation of ingested carbon by *E. pacifica* was high 84%; range 66–95%) in 23 out of 24 animals. One animal that assimilated only 46% is not included in the average because the food left in the foregut made up an abnormally large unassimilated fraction that could have been digested later.

A large fraction of the ingested carbon (average, 25.6%) appeared in the tissues of almost every animal in spite of the fact that there was usually insufficient carbon to satisfy all the carbon demands of the animal. Apparently, the euphausiid does not use all incoming carbon for respiration, but rather draws upon its own tissues to make up for any metabolic deficit. In those where sufficient carbon was supplied as food, short-term efficiencies were similar to those obtained by growth experiments in the laboratory where molt carbon was included as part of the incorporation of carbon.

FOOD AND FEEDING

A euphausiid must capture food particles of sufficient size and carbon content and at an adequate rate to satisfy its carbon requirements. Laboratory experiments have shown that *E. pacifica* is capable of eating from suspension either algae or small nauplii, and in her recent book Ponomareva (1963) listed a variety of phyto- and zooplankters found in the thoracic baskets of this species. In an earlier paper, Ponomareva (1955) stated that phytoplankton do not play an important role in the feeding of *E. pacifica* although some

TABLE III. Carbon budget of *E. pacifica* determined with carbon-14. Catabolic carbon = incorporated carbon + intestine carbon + egested carbon. All weights in milligrams.

		Weight of carbon				Weight of carbon				
Animal No.	Dry weight animal	offered as *Artemia*	ingested	incorporated	Per cent C incorporated	in intestine	egested	catabolized including CO_2	respired (calculated from RQ = 0.8)	Percent C assimilated
1	7.394	.0553	.0456	.0167	36.6	.0044	.0018	.0227	.101	86
2	7.668	.0553	.0308	.0036	11.7	.0016	.0001	.0255	.106	94
3	4.614	.0553	.0338	.0070	20.7	.0017	.0006	.0245	.067	93
4	3.515	.0553	.0406	.0142	35.0	.0021	.0008	.0235	.055	93
5	8.892	.1106	.0998	.0456	45.7	.0070	.0047	.0425	.146	88
6	7.360	.2765	.0915	.0200	21.9	.0081	.0133	.0501	.107	77
7	6.138	.2765	.1004	.0295	29.4	.0098	.0141	.0497	.089	78
8	5.747	.2765	.2317	.0919	39.7	.0119	.0244	.1035	.084	84
9	6.998	.2765	.0527	.0164	31.1	.0077	.0067	.0279	.101	73
10	6.028	.2765	.1496	.0255	17.1	.0105	.0020	.1116	.087	92
11	7.305	.2765	.0894	.0095	10.6	.0040	.0008	.0751	.106	95
12	8.072	.2765	.1403	.0246	17.5	.0143	.0034	.0980	.117	87
13	7.440	.2765	.1817	.0419	23.1	.0188	.0194	.1016	.108	79
14	9.522	.5530	.4206	.1686	40.1	.0529	.0238	.1753	.138	82
15	2.652	.0338	.0168	.0036	21.4	.0008	.0003	.0121	.040	93
16	4.978	.0553	.0317	.0098	30.9	.0050	.0019	.0150	.076	78
17	4.652	.0553	.0491	.0126	25.7	.0088	.0031	.0246	.037	76
18	6.554	.0205	.0180	.0083	46.1	.0046	.0016	.0035	.102	66
19	3.250	.0553	.0305	.0078	25.6	.0033	.0015	.0179	.047	84
20	2.555	.0553	.0245	.0076	31.1	.0024	.0011	.0133	.038	86
21	1.275	.0830	.0149	.0008	5.5	.0000	.0000	.0141	.020	80
22	2.033	.1106	.0497	.0076	15.3	.0255	.0013	.0153	.031	46
23	3.532	.0553	.0458	.0071	15.4	.0032	.0060	. 295	.056	80
24	4.601	.1106	.0557	.0053	9.5	.0039	.0073	.0391	.072	80
				Average:	25.6				Average:	84[a]

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[a] Exclusive of animal No. 22; see text.

do feed on phytoplankton in the spring. She found that feeding is confined to the upper 100 m of water and occurs at night and in the evening. Deeper than 500 m there is little or no feeding.

Because *E. pacifica* is omnivorous, the feeding behavior of individuals on diets of unicellular algae and *Artemia* nauplii was examined. It became evident that several important factors affect feeding by *E. pacifica.*

PARTICLE SIZE

The size of the food particle governs to a great extent whether a euphausiid will succeed in ingesting it. Individual *E. pacifica* were fed experimentally a known number of newly hatched *Artemia* daily except for 1 day when *Artemia* which were 5–6 days post-hatch (750 μ long) were presented to the animals (Table IV). *Euphausia pacifica* drastically reduced its intake when it was fed large nauplii. In 22 additional experiments where 500 newly-hatched nauplii were presented to individual animals the average number ingested was 52 nauplii per milligram dry weight euphausiid per day; in four experiments where 500 large *Artemia* nauplii were presented to individual euphausiids they ate on the average only five nauplii per milligram euphausiid per day.

EFFECT OF MOLTING ON FEEDING

When *E. pacifica* molted during a feeding experiment fewer nauplii were eaten during the day of molt (Table IV). Thus, molting acts as a depressant to feeding.

TABLE IV. Feeding of individual *E. pacifica* on *Artemia* nauplii as affected by euphausiid molting and the size of the nauplii. All animals were fed newly hatched (0.375-mm) nauplii except on day 7 when 0.75-mm nauplii were substituted.

Animal No.	Dry weight of animal (*mg*)	Nauplii	Day							
			1	2	3	4–6	7	8	9	10
1.	3.519	No. offered	600	610	600	1010	500			
		Per cent eaten	33	54	5[a]	30	2			
2.	5.575	No. offered	500	500	500	1000	515	500	500	700
		Per cent eaten	34	39	7[a]	90	7	14[a]	30	18
3.	5.000	No. offered	1000	500	1015	1000				
		Per cent eaten	20	34	34	25[a]				
4.	1.836	No. offered		500	500	1020	500	500	500	700
		Per cent eaten		21	1[a]	49	1	7	10[a]	21
5.	4.578	No. offered		500	500	1000	500	500	500	700
		Per cent eaten		67	45	44	2	42	22[a]	23

[a] Molted.

Density of the Food Organisms

An adult *E. pacifica* can ingest all or nearly all of 50 *Artemia* nauplii in 100 ml of sea water over a 24-hr period in the dark. When the volume of sea water is increased while the number of nauplii is kept constant, the effect of density of food organisms can be determined and recorded as milliliters of water cleared per animal per hour (F). The animals chosen for this experiment were well fed and had molted 1 or 2 days earlier. The results (Fig. 11) indicated that the median "filtering rate" was highest (45 and 43 ml per animal per hour) at densities of one nauplius in 20 ml and 40 ml, respectively. However, a further decrease in density to one nauplius in 60 ml presented the animal with a more severe food-catching problem, and the median filtering rate diminished to 22 ml per animal per hour, although some euphausiids were still moderately successful. The high filtering rates obtained with diets of *Artemia* nauplii were never obtained in experiments where algae were fed. Euphausiids probably can sense and capture their prey and the so-called "filtering rate" is more properly a capture rate dependent upon factors other than random swimming and sweeping clear a volume of water as expressed in the Gauld equation. The decrease in density may impose a detection problem on the euphausiid by increasing the mean distance between it and its food particle. If so, then the critical distance between an adult *E. pacifica* and its food is about 1.7–2 cm, beyond which the euphausiid becomes inefficient at detecting and capturing prey in the dark.

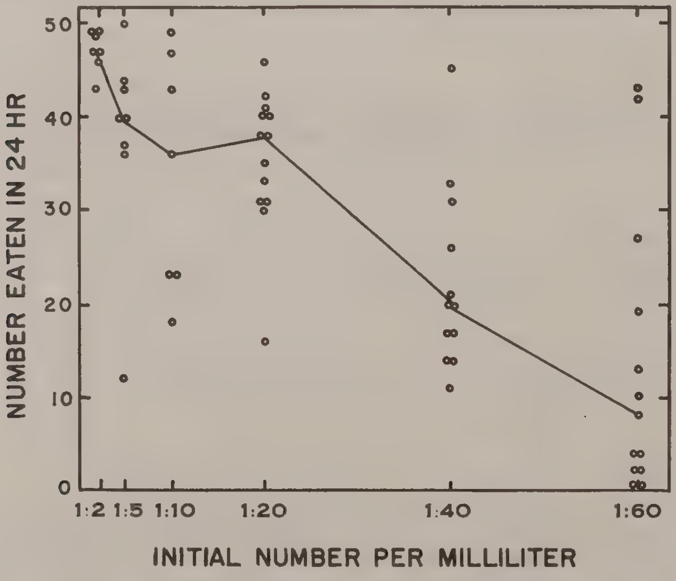

Fig. 11. The relation between density of *Artemia* nauplii and the number eaten by adult *E. pacifica*. Each animal was presented with 50 newly-hatched *Artemia* nauplii in sea water adjusted in volume to provide the densities indicated. The line is drawn through the median values.

FOOD SELECTION

Anraku and Omori (1963) found that some copepods, e.g. *Centropages hamatus* and *C. typicus*, although omnivorous, decreased their feeding on the diatom *Thalassiosira fluviatilis* to feed on *Artemia* nauplii available at the same time. *Euphausia pacifica* behaved similarly, showing distinct preference for nauplii over the diatom. In 17 experiments *Thalassiosira* was fed to *E. pacifica* at a concentration of 15×10^3 cells/ml; 500 *Artemia* nauplii were added in each of six of these; the filtering rates on *Thalassiosira* over 24 hr were recorded in both situations. Feeding on the diatom was depressed (median $F = 0.3$) over the controls (median $F = 1.9$) when *Artemia* was present ($P < 0.01$; Wilcoxin "*t*" test).

In another series of experiments, feeding on *Dunaliella tertiolecta* alone was alternated with feeding on *Dunaliella* plus 500 *Artemia* nauplii. The results (Table V) show that feeding on *Dunaliella* was suppressed or even eliminated when the euphausiid had brine shrimp nauplii available.

Euphausia pacifica may select among different copepod food organisms in the sea. Ponomareva (1955) compared the percentage composition of copepods in water being grazed by euphausiids with that in the thoracic baskets of euphausiids from the same water. Some copepod species, e.g. *Metridia pacifica* and *Calanus tonsus*, were eaten to a greater degree than their relative abundance in the water would give cause to expect. *Oithona similis*, a copepod of the proper size range for ingestion and present in large numbers, was rarely eaten.

TABLE V. Filtering rates[a] of *E. pacifica* on 15×10^3 cells/ml of *Dunaliella tertiolecta* in 500 ml with and without *Artemia* nauplii present. Days are consecutive.

Animal No.	Dry weight of animal (*mg*)	Filtering rate on *Dunaliella*		Number of nauplii eaten on day 2	Per cent eaten of all nauplii offered
		Day 1 *Dunaliella* alone	Day 2 *Dunaliella* and *Artemia*		
1	1.7	1.3	0.4	31	6
2	5.3	10.5	0.8	252	50
3	4.9	1.4	0.1	42	8
4	4.3	24.9	0	65	13
5	4.4	2.3	0	304	61
		Dunaliella alone			
6 (control)	3.8	2.3	1.6[b]	–	–

[a] Milliliters cleared per animal per hour.

[b] On the third day the filtering rate remained 1.6 for the control organism.

INDIVIDUAL VARIABILITY

An experiment was performed to observe the feeding characteristics of individual *E. pacifica* over relatively short time intervals. Four animals (A, B, C, and D, Fig. 12) were given 50 *Artemia* nauplii each in 100 ml of membrane-filtered sea water at 10 C (membrane pore size, 0.45 μ). Because molting depresses feeding (see above) only animals that had molted at least 24 hr earlier were used. These experiments were done only in the dark or under a red light when the nauplii were counted. Short-term variations occurred in the feeding rate and each individual appeared to feed differently. Animal A devoured nauplii at a steady rate, 1–2 nauplii/hr; animal B ate half of the nauplii in the first 4 hr and thereafter ate at a constant rate. Although not indicated by the ingestion curve in Fig. 12, animal C killed many nauplii without devouring them so that the curve should more closely approximate that of animal B; animal D ate more than half of the nauplii between the 8th and 12th hr of the experiment.

These results illustrate the variability of individual feeding in this organism. All subsequent experiments are presented as rates over a single day and therefore represent an average of differing short-term rates.

PARTICULATE FEEDING

I calculated how many nauplii of a size and carbon content equivalent to an *Artemia* nauplius (5.5×10^{-4} mg C/nauplius) must be captured and eaten

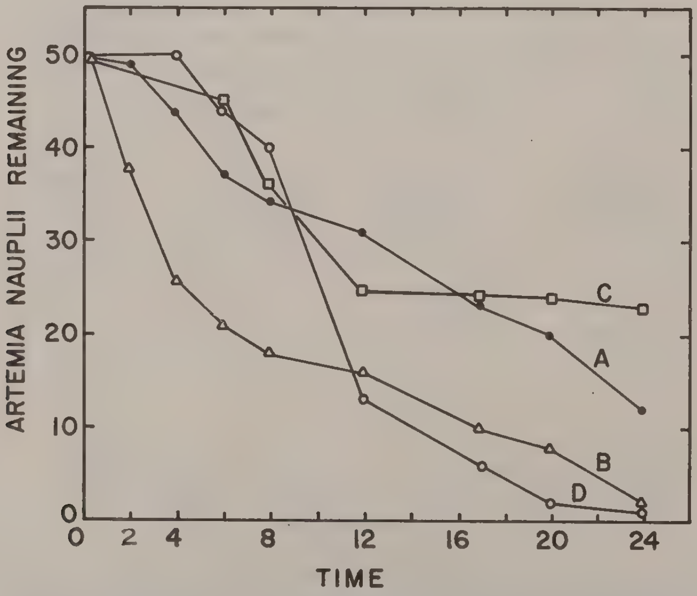

FIG. 12. Feeding of four individual adult *E. pacifica* on *Artemia* nauplii recorded at short intervals over a 24-hr period. The initial density of nauplii was 50/100 ml.

in the sea to satisfy the euphausiid's carbon requirements for growth, molting, respiration, and digestive inefficiency. The 0.24-mg juvenile needs 12 nauplii/day and the largest animal considered, 9 mg, must capture 336 per day (Table VI). Under laboratory conditions these numbers were easily captured because the density of nauplii was maintained as high as 4–5 nauplii/ml. Comparable densities have not been reported for the sea. The euphausiid may meet its food requirements by feeding on aggregations of food organisms as reported by Ponomareva (1954).

GRAZING

McAllister et al. (1960) investigated the primary productivity of the northeastern Pacific Ocean within the subarctic water mass, about 500 miles from the nearest part of the continental shelf, and in a region where *E. pacifica* is found in moderate abundance and near an area where maximum concentrations of this species have been observed (Brinton, 1962). During the summer period of productivity, they found detrital carbon equivalent to 0.1–0.2 mg C/liter and plant carbon between 0.01 and 0.035 mg C/liter. Production was about 0.007 mg C per liter per day. From the values of total carbon obtained by McAllister and coworkers I calculated (Table VI) the amount of grazing on phytoplankton and detritus required by individual *E. pacifica* of different weights to maintain their metabolism and growth in nature. If the total amount of particulate organic carbon available is considered as the food source, ca. 0.16 mg C/liter (detritus and phytoplankton) and uniformly distributed, a 0.24-mg animal would need to filter 43 ml/day (F = 2 ml per hr per animal)

TABLE VI. Nauplii required by *E. pacifica* and filtering rates on phytoplankton and detritus in ocean, to provide carbon needed at various levels of growth. Filtering rates based on 0.16 mg particulate carbon per liter in northeastern Pacific Ocean, summer (see text), calculated on basis of 90% assimilation of ingested carbon.

Dry weight of animal (*mg*)	C requirement/day in g $\times 10^{-5}$	*Artemia* nauplii needed per day	Milliliters of sea water animal must clear per hour to satisfy requirement
0.24	.68	12	2
1.0	2.4	48	6
2.0	4.6	96	12
3.0	6.6	120	17
4.0	9.2	168	24
5.0	11.0	192	29
6.0	14.0	264	36
7.0	15.0	264	39
8.0	18.0	336	47
9.0	19.0	336	49

and the 9-mg animal would need to filter 1170 ml/day (F = 49 ml per hr per animal). Filtering rates for intermediate animals are presented in Table VI.

Because *E. pacifica* is omnivorous it is likely that both detritus and phytoplankton are eaten when no prey, e.g. nauplii, are available. Experiments were performed, therefore, to indicate the ability of the euphausiid (dry weight = 2.8–5.1 mg) to filter water containing phytoplankton cells. The rates obtained (Table VII) varied considerably from animal to animal; the maximum rate was 38 ml/hr for a 4.3 mg animal on a dilute suspension of *Platymonas*. The average rate on *Platymonas* was 7 ml per mg euphausiid per hr or 168 ml per mg euphausiid per day. On a diet of *Gonyaulax polyedra* the average rate for three animals was 3.5 ml per mg per hr or 84 ml per mg per day. Three animals feeding on *Thalassiosira* showed markedly lower filtering rates, averaging 0.79 ml per mg per hr or 19 ml per mg per day. The low rates with *Thalassiosira* seem to reflect rejection of this species by *E. pacifica*. Often no cells of this species of alga were eaten whereas cells of *Platymonas*, *Dunaliella*, or *Gonyaulax* were always taken.

TABLE VII. Filtering rates of *E. pacifica* on unicellular algae. Twenty-four-hour experiments in 1 liter of sea water between 10 and 13 C.

		Filtering rate	
Dry weight of animal (*mg*)	Number algal cells/ml	Ml/hr	Ml/mg euphausiid/hr
Platymonas subcordiformis			
2.8	1,600	32	11.5
3.5	1,700	18	5.2
4.9	2,000	12	2.4
4.3	3,600	38	8.8
Gonyaulax polyedra			
5.1	6,400	17	3.4
3.8	6,500	20	5.4
3.9	14,700	6.7	1.7
Thalassiosira fluviatilis			
5.2	15,600	2.8	0.5
5.0	16,800	2.3	0.5
5.2	17,100	7.1	1.4

In four experiments the number of *Thalassiosira* was adjusted (7.3×10^3 cells/ml) so that the total volume of the cells equalled the total volume of the cells of *Dunaliella* (41×10^3 cells/ml) used. (Cell volumes were determined by Mullin et al. (1966).) The filtering rates (milliliters cleared per hour) were:

		Day and food				
Animal No.	Dry weight (*mg*)	1 *Dunaliella*	2 *Thalassiosira*	3 *Dunaliella*	4 *Dunaliella*	5 *Dunaliella*
1.	3.0	2.2	0	1.7	1.5	–
2.	3.0	2.6	0	0.2	1.6	–
3.	2.7	–	2.0	3.7	1.6	0.6 (molted)
4.	3.8	–	0.4	2.3	1.6	1.6

Two of the euphausiids (No. 1 and 2), conditioned to feeding on *Dunaliella*, did not filter *Thalassiosira* the following day when no *Dunaliella* were present. *Dunaliella* was offered without *Thalassiosira* on the third day; one animal resumed feeding immediately but the other did not eat until the fourth day. Thus, a lag effect seemed to be induced by exposure to *Thalassiosira* in one animal. Euphausiids No. 3 and 4 commenced filtering when *Thalassiosira* was offered first. The filtering rate increased substantially the next day, when only *Dunaliella* was offered.

The filtering rates may be misleading as far as the capacity for food-getting by an individual euphausiid is concerned. In dense suspensions of algae the euphausiid can fill its foregut, gland, and intestine quickly so that effective filtration drops to practically nothing in a few minutes. On a diet of *Dunaliella* (10^6/ml) a euphausiid can pack its foregut and gland within 10 min. The first fecal pellet is formed and passed within 1 hr and if the animal is subsequently starved the foregut may still retain a trace of green plant matter after 2 days. If *Artemia* are caught and eaten by the euphausiid just after the digestive tract has been crammed with algae, digestion seems to be accelerated; within 6 hr no trace of chlorophyll remains in the digestive tract. Animals with full digestive tracts observed immediately after collection at sea did not fully empty their foreguts even after 24 hr without feeding. At minimal feeding (50 *Artemia* nauplii) some food was still in the foregut after 40 hr. When a surplus of nauplii was fed over the same period to other individuals of the same batch no trace of the former food remained in the foregut.

The total amount of particulate carbon available in the sea is adequate to maintain *E. pacifica* at the filtering rates determined in the laboratory. Phytoplankton cells alone would not suffice (Bainbridge, 1957). It is more likely, however, that *E. pacifica* depends in large part upon its ability to exploit aggregations of copepods than on its marginal ability to filter enough carbon from a dilute suspension.

GENERAL DISCUSSION

Several interesting features of euphausiid feeding were brought out in this investigation. Selective feeding is not new but now can be extended to the euphausiids. These experiments give the impression that the euphausiid may have a great sensory capacity for detecting food organisms in the surrounding water. The thoracic basket of the euphausiid is its filtering mechanism. The effective opening into the basket of a 3.5-mg animal is 3 mm^2. An opening of this size can filter 21 ml/hr at a cruising speed of 2 cm/sec or 42 ml/hr at a cruising speed of 4 cm/sec. These cruising speeds were observed for this euphausiid in the laboratory. Occasionally, speeds up to 18 cm/sec were attained by adult animals but only for 1 or 2 sec. The aforementioned filtering capability permits achievement of the median filtration rates of 45 and 43 ml/hr, which were calculated for *E. pacifica* feeding on *Artemia* nauplii at a nauplii density of 1 in 20 ml and 1 in 40 ml, respectively. The median rate decreased sharply, however, when only one nauphius/60 ml was offered (Fig. 11); a sensory mechanism with a finite range may be used by the euphausiid for capturing nauplii.

Euphausia pacifica seems to become conditioned after feeding on a particular food and neglects other food organisms which are acceptable on other occasions, but less desirable. In several experiments a day or more elapsed before a euphausiid previously fed on *Artemia* began to feed on suspended algae. This behavior did not seem to be a case of "filling up" because feeding on *Artemia* continued unabated in densities of 2–3 nauplii/ml and digestion was rapid. Thus, the food available and the animal's inclination to feed on the food are factors which must be considered in relating phytoplankton carbon production to incorporation of this carbon into the zooplankton.

Two assessments of carbon transfer were made in this study. In the laboratory, rapidly growing *E. pacifica* can assimilate as much as 90% of the carbon they ingest and incorporate as much as 30% of the assimilated carbon into their tissue. This efficient utilization of carbon may never be realized for the majority of individuals in the ocean and the incorporation is probably nearer to 10% of the assimilated carbon.

Some observations were made on the molting of *E. pacifica* which are important to this discussion. Molting seems to be confined to the night time and, in laboratory containers, molts are degraded to a softened, easily torn condition within 24 hr, probably by bacterial action. The sinking rate of intact molts, determined in sea water at 10 C and 33‰ salinity, was about 1 m in 5 min. Thus, molts may drift down almost 300 m in a day when undisturbed. If euphausiid ecdysis in the sea occurs only at night, then molts which are released in the upper 100 m persist at least through 1 day between the surface and 400 m.

The carbon incorporated and released as part of spawned eggs represents no real loss to the planktonic food chain because the eggs remain available to grazers or develop further. If the molts are eaten, then the amount of organic carbon available to the next step(s) in the food chain is about 30% of that ingested throughout the life span of euphausiids. Should the molts drift out of the system uneaten, the carbon available to predators in the bodies of the euphausiids and their eggs is about 19% of that which was orginally eaten by the euphausiids.

In an earlier paper (Lasker, 1964), I suggested that molts might contribute substantially to the detritus of the ocean. Detritus, as Krey (1961) stated, may contribute from 40 to greater than 90% of the organic matter in ocean regimes; McAllister et al. (1960) recorded that 80–90% of the organic matter in the northeastern Pacific Ocean was detrital. The chemical composition of detritus suggests that it is of animal origin (Parsons and Strickland, 1962).

The contribution to detritus by molting may be viewed in two ways. First, the 10% of the dry weight of each euphausiid shed every 5 days gives the figure of approximately one euphausiid biomass released to the sea every 50 days as molts. In 1 year this total may be seven times the euphausiid biomass. Secondly, Jerde and Lasker (1966), using the wet biomass figure for *E. pacifica* (1 g/m^2) supplied by Dr E. Brinton, calculated that 1.5 g per m^2 per year is dropped as molt dry weight over the euphausiid's range (1.3×10^{13} m^2). In terms of organic carbon this is 0.3 g C per m^2 per year or 0.4% of the actual carbon production of the euphotic zone in the summer as reported by McAllister et al. (1960). The facts that other euphausiid species contribute to the zooplankton biomass, that biomass estimates are low, that other crustaceans are molting, and that primary production is lower in the winter, indicate that 0.4% is a minimal figure.

Because of the regularity of molting it is tempting to suggest that molts might be used to estimate the biomass of euphausiid shrimps. The chief problem of biomass estimates from plankton net collections is the avoidance behavior of zooplankters (Fleminger and Clutter, 1965); molts do not present this problem. Molts are caught in plankton nets but usually are ignored later by the investigator. Yet this study has shown that two important features of a euphausiid besides its identification can be told from its molt: dry weight and body length. Only the tail of the molt need be caught with the uropods and telson intact. Thus, information on size, weight, and numbers of different euphausiid species may be ascertained in this way, given data on molt residence time in the water column.

The live biomass of *E. pacifica* alone over the area in which it occurs in the Pacific Ocean is equivalent to 0.11 g C/m^2. About 5% of the carbon in the standing crop of *E. pacifica* is needed to maintain the growth, respiration, and molting of the population per day; therefore, 5.5 mg C per m^2 per day is ingested by the population. The mean daily primary production of the euphotic zone in the summer in the northeastern Pacific Ocean was reported by McAllister et al. (1960) to be about 205 mg C per m^2 per day. Therefore, about 3% of the production is ingested by *E. pacifica* alone, but not until the carbon has passed a previous step in the food chain, i. e. through a smaller, herbivorous crustacean.

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Effects of Salinity and Temperature on Survival and Development of Larval Atlantic Menhaden, *Brevoortia tyrannus*

INTRODUCTION

Atlantic menhaden are subject to a wide range of salinity during early stages of development. Most evidence indicates that this species spawns principally along the middle and south Atlantic Coast of the United States during the winter, some distance offshore (Reintjes, 1961; Massmann, Norcross, and Joseph, 1962). After hatching at sea, larvae enter the estuaries and move into the upper tidal areas of tributary streams where they develop into juveniles (June and Chamberlin, 1959). From the time they hatch until they reach the nursery areas, larvae run the gamut of salinities from about 35‰ to about 1‰ (Reintjes and Pacheco, 1966).

Water-development projects and pollution are becoming more prevalent as the human population grows. For example, dams that will effect large masses of water in estuaries on the Atlantic and Gulf coasts of the United States are under consideration. These structures will probably reduce the nursery areas accessible to menhaden larvae and may reduce the numbers of menhaden. Therefore, it is important to learn what happens to larvae that are prevented from reaching a low-salinity environment.

Laboratory experiments were designed to ascertain the effects of salinity and low temperature on the survival and growth of menhaden larvae. During 1964, experiments at Beaufort, North Carolina, yielded information on the temperature tolerance of Atlantic menhaden larvae at a fixed salinity (Lewis, 1965). The study reported here consisted of two experiments. The objective of the first was to determine the effect of various levels of salinity at low temperatures on the survival of menhaden larvae, those of the second were to determine (1) if larval menhaden will transform into normal juveniles in salinities of 15‰ and greater, and (2) if they transform, it is important to know what effect exposure to these salinities has on their development.

An anchored net, 12 m long, 2.5 m deep, and constructed of 3-mm-diameter mesh with a large bag leading into a floating box, was used during daylight to trap and hold larvae for the experiments. More specimens were obtained in less time than in 1964, when larvae were collected at night on flood tides with a plankton net that funneled into a similar box.

COMBINED EFFECTS OF SALINITY AND LOW TEMPERATURE

Equipment and procedures.—The holding, acclimation, and test tanks were the same as used in 1964 (Lewis, 1965), except that sea water was filtered through synthetic sponges rather than glass wool and marble chips. Temperature in the acclimation tank and in the three fiber-glass test chambers was controlled by a Thermistemp and thermistor probe made by the Yellow Springs Instrument Company.[1] Use of this equipment made possible the rapid adjustment of temperatures for each new test. Salinity was measured by a hydrometer and adjusted to the desired concentration by adding distilled water. Well water was used for the tests in fresh water. Dissolved oxygen, checked periodically in all test containers, ranged from 80% to 95% saturation. Larvae were fed 1- and 2-day-old nauplii of *Artemia salina* daily. All larvae fed, except those under stress. Larvae were tested at temperatures of 2 to 6 C (by 1-degree intervals) and at salinities of 0 to 30‰ (by 5-‰ intervals). Prior to each test they were acclimated at temperatures of either 10 or 15 C and salinity of 25 to 30‰ for 102 ± 84 hours. At this stage of life history menhaden appear to acclimate in but a few hours as they feed well and no mortality occurs. Limited facilities,

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[1] The Bureau of Commercial Fisheries neither recommends nor disapproves the products referred to in this paper.

TABLE 1.—*Number of hours to 50% mortality of menhaden larvae acclimated at 10 C and held at different combinations of temperature and salinity*

Test temperature Celsius	Salinity ‰						
	0	5	10	15	20	25	30
2	4.2	14.2	27.5	34.0	25.0	21.5	15.2
3	4.2	33.0	59.0	77.6	53.2	40.0	26.5
4	7.0	>96.0	>96.0	>96.0	>96.0	>96.0	35.0
5	7.8	>96.0	>96.0	>96.0	>96.0	>96.0	>96.0
6	13.0	>96.0	>96.0	>96.0	>96.0	>96.0	>96.0

tight scheduling of experiments, and ready availability of material caused wide variation in acclimation time.

Results.—As in the 1964 tests, when larvae entered a chill coma they lost their equilibrium, floated, and twitched erratically. At salinities of 5‰ and less some larvae died with their mouths wide open, indicating a convulsive death; all turned stiff and milky-colored immediately after dying.

Results of the 10 C acclimation series (Table 1) indicated that under natural conditions larvae can be expected to survive for approximately 1 day in water of 2 C and 10 to 25‰ salinity, and 2 or 3 days at 3 C and 10 to 20‰ salinity. Larvae probably would live for only a few hours at temperatures of 6 C and below in fresh water (0‰), whereas the probability of survival generally would be good at temperatures of 4 C and above, and salinities between 5 and 30‰.

Larvae acclimated at 15 C and held at 2 C survived almost 2 days in a salinity of 10‰, and 1 day in 15‰ (Table 2). Survival at 2 C was less than 1 day in other salinities tested. At 3 C, larvae survived approximately 2 days in salinities between 5 and 20‰. As in the 10 C acclimation series, larvae survived only a few hours in 0‰ salinity. In both acclimation series, the lower and upper limits of salinity tolerance increased with increasing temperature.

Bishai (1961) found that newly hatched larvae of herring, *Clupea harengus*, can live at salinities as low as 2.5‰, and that they live longer in salinities of 10 to 15‰ than in higher or lower salinities. In general, these findings agree with the results of the present experiments on menhaden larvae.

EFFECTS OF HIGH SALINITY

Equipment and procedures.—Approximately 25 larvae of uniform size, acclimated at 25 to 30‰ salinity, were held in each of six 34-liter polyethylene tanks at salinities of 15, 20, 25, 30, 35, and 40‰. Since larvae transferred directly into water at 35 and 40‰ salinity soon died, tests at these two levels actually were started at 30‰ salinity. The salinity was then gradually raised each day by slowly adding a solution of concentrated sea water until the desired salinities of 35 and 40‰ were reached at the end of a week; no mortality occurred. Salinities were maintained at the test level by the addition of distilled water. Compressed air was used to oxygenate the water and to recirculate it through a filter of charcoal and glass wool. This experiment was started 7 April 1965 and completed 4 June 1965. As in the first experiment, menhaden were fed nauplii of 1- and 2-day-old *Artemia salina*.

Results.—All larvae did not grow at the same rate. Although each tank contained only larvae at the beginning of the experiment, both juvenile and larval forms were present at the end. The differences in size of fish at completion of the experiment may have been due to the consumption of more food by the more aggressive individuals or other unknown metabolic causes. When *Artemia* were introduced, all fish appeared to feed actively, and sufficient *Artemia* were available for all. All the specimens in 20 and 25‰ salinity died during the experiment from unknown causes.

The experiment indicated that larvae will transform into juveniles at higher salinities than are found in most nursery areas. Salinity tolerance of the larvae may be comparable with that demonstrated for herring by Holliday and Blaxter (1960). They showed that eggs and larvae of herring have a wide salinity tolerance and are capable of maintaining the concentration of tissue fluids within relatively narrow limits when subjected to a wide range of salinities.

TABLE 2.—*Number of hours to 50% mortality of menhaden larvae acclimated at 15 C and held at different combinations of temperature and salinity*

Test temperature Celsius	Salinity ‰						
	0	5	10	15	20	25	30
2	4.5	15.8	46.0	26.8	16.2	14.0	10.2
3	6.0	44.5	53.0	56.0	51.2	27.0	10.5
4	4.5	26.2	>96.0	>96.0	>96.0	39.5	14.0
5	7.2	50.5	>96.0	>96.0	>96.0	>96.0	48.0
6	8.8	>96.0	>96.0	>96.0	>96.0	>96.0	>96.0

EFFECTS OF SALINITY ON VERTEBRAL DEVELOPMENT

Fish held at salinities of 15, 20, 25, 30, 35, and 40‰ were X-rayed to determine if salinity affected their vertebral development. All vertebral counts fell within the limits described for fish from North Carolina (Sutherland, 1963). Approximately one-third of the specimens in each of the test salinities showed abnormalities (single or double curvature) of the spine. Compression of vertebrae resulted in the bulging of centra in some specimens. These abnormalities, not found in samples of larvae prior to the start of the experiment, may have been partly due to specimens being held in an environment of 15‰ salinity and greater, or to a diet of *Artemia* only. Generally, menhaden are not found in such high salinities in the nursery area until they start their return to the sea as juveniles. The same abnormalities were observed by Bureau biologists in specimens of juvenile *Brevoortia smithi* collected earlier from water of approximately 40‰ salinity in Buttonwood Canal, Flamingo, Florida.

SALINITY–TEMPERATURE RELATION

Results of the two acclimation series in the temperature–salinity experiment indicated that if larvae enter an estuary during the winter or early spring, when water temperatures may approach the freezing point, they will have the best chance of survival if the water temperature does not fall below 4 C and salinity remains between 10 and 20‰. Brawn (1960), testing the survival of herring, *Clupea harengus*, at temperatures between 6 and 9 C, suggested that adverse effects of salinity were minimal at levels above 5‰.

Field observations were made periodically during 1965 to determine what salinities and temperatures are encountered by menhaden larvae in a nursery area. Larvae entered one such area, Bath Creek, North Carolina, a tidal tributary of the Pamlico River, when the water temperature was approximately 9 C and the salinity less than 5‰. While they were in the area, prolonged rainfall and runoff lowered the salinity to 1‰ or less, and the water temperature rose to 30 C. Pacheco and Grant (1965) studying a tributary of Indian River, Delaware, found larvae at temperatures ranging from 3 to 32 C and salinities of less than 1 to 30‰.

The experiments in which larvae were held at salinities of 15 through 40‰ suggested that larval menhaden can survive and transform into juveniles even if they are forced to remain in a more saline environment than characterizes most nursery areas. Such fish might undergo slight malformation of the vertebral column, but the resulting abnormalities would probably not prevent them from otherwise growing normally. Results also indicate that in these higher salinities some larvae were retarded in growth.

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Fecundity of the Striped Bass, *Roccus saxatilis* (Walbaum)

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Fecundity of the Striped Bass, *Roccus saxatilis* (Walbaum)

INTRODUCTION

Investigators of striped bass long have needed a method for the quick and reliable estimation of the number of mature ova released by a spawning population. Jackson and Tiller (1952) counted the eggs in striped bass from the Chesapeake Bay area and showed the relation of egg number to weight, length, and age of the fish. They did not, however, make a statistical comparison to determine which of these attributes most accurately indicated the number of mature ova produced. The objective of the present study was to find an easily measured feature, such as weight, length, or age, that constitutes a good index of fecundity.

During spring spawning runs in the Roanoke River, North Carolina, we collected 159 female striped bass from the commercial catch; 12 in 1958, 17 in 1960, and 130 in 1963. To reduce the possibility of their being partially spawned, we used only fish caught below the spawning area as they moved upstream. The fork length and weight of each fish were measured to the nearest 0.1 inch and 0.1 lb. The ovaries were preserved in 7 to 10% formalin. Ages were determined later by counting the number of annuli on plastic impressions of the scales. If no annulus was present at the edge of the scale, a "virtual" annulus was added. For example, fish that had four annuli and had completed another year's growth were assigned to age-group V.

DISTRIBUTION OF MATURE OVA WITHIN AND BETWEEN OVARIES

Spawning by an individual striped bass probably is completed within a few hours. Mature ova must therefore be positioned within an ovary so as to permit their release over a short period of time. Thus, accurate estimation of the number of these ova is aided by some knowledge of their actual distribution within an ovary.

Scofield (1931), working with striped bass on the West Coast of the United States, and Merriman (1941) and DeArmon (unpublished), who studied the same species on the East Coast, found mature ova uniformly distributed throughout both ovaries. To determine if this was also true for striped bass from the Roanoke River, we counted only ova that would have been released during the current spawning season. These were mature,

TABLE 1.—*Estimated mean number of mature ova (thousands) by age-group and body weight in striped bass from the Roanoke River, North Carolina, during April and May 1958, 1960, and 1963*

[Values in parentheses are the numbers of specimens upon which the mean values are based. These numbers do not total 159 because the weight of 1 fish and the lengths of 12 fish were not recorded. Sixteen fish could not be aged]

Body weight (pounds)	Age-group									
	IV	V	VI	VII	VIII	IX	X	XI	XII	XIII
2.0–2.9	130 (2)	231 (1)	–	–	–	–	–	–	–	–
3.0–3.9	251 (8)	–	–	–	–	–	–	–	–	–
4.0–4.9	328 (29)	295 (3)	345 (1)	–	–	–	–	–	–	–
5.0–5.9	401 (21)	458 (4)	289 (1)	–	–	–	–	–	–	–
6.0–6.9	390 (3)	436 (4)	586 (2)	–	518 (1)	–	–	–	–	–
7.0–7.9	–	422 (3)	622 (2)	548 (1)	–	–	476 (1)	–	–	–
8.0–8.9	642 (1)	878 (1)	684 (1)	512 (2)	688 (3)	–	–	–	–	–
9.0–9.9	–	–	845 (1)	701 (3)	790 (5)	855 (1)	903 (1)	–	–	–
10.0–10.9	–	–	960 (1)	828 (11)	1,102 (2)	840 (3)	–	835 (1)	–	–
11.0–11.9	–	–	–	–	838 (2)	898 (1)	863 (1)	–	–	908 (1)
12.0–12.9	–	–	–	–	1,075 (1)	981 (5)	–	795 (1)	–	–
13.0–13.9	–	–	–	–	–	–	1,120 (1)	–	–	–
14.0–14.9	–	–	–	–	–	825 (1)	1,043 (1)	1,199 (1)	1,136 (1)	–
15.0–15.9	–	–	–	–	–	–	1,055 (1)	1,029 (1)	–	–

opaque ova measuring at least 0.70 mm (Lewis, 1962). The quantity of mature ova in each sample was expressed as the number per gram of ovary.

After the preserved ovaries were drained of excess moisture, blotted, and weighed to the nearest 0.1 g, samples of ova were taken from the anterior, central, and posterior sections of each ovary, then covered in 90-mm Petri dishes to prevent dehydration. Approximately 1 g of each sample was removed and weighed on an analytical torsion balance to the nearest 0.001 g. The ova were then teased apart and the mature ones counted with the aid of a 3× desk magnifier–illuminator.

The mean numbers of mature ova per gram of ovary in samples from the three sections of each ovary were compared by analysis of variance. In material from each of the three study years, no significant differences were detected among sections of the same ovary or between the left and right ovaries. Thus, a single mean value, based on the three samples, was computed for each ovary. To estimate the total number of mature ova for each ovary, we multiplied the mean number of mature ova per gram by the total ovary weight. We then added the estimated number of ova from each ovary to obtain the total for each fish.

RELATION OF FECUNDITY TO BODY WEIGHT, FORK LENGTH, AND AGE

The mean number of mature ova in striped bass from the Roanoke River varied considerably by age-group, body weight, and fork length (Tables 1, 2, and 3). Morgan and Gerlach (1950) showed that striped bass in Oregon produced about 100,000 eggs per pound of body weight. In striped bass from

TABLE 2.—*Estimated mean number of mature ova (thousands) by age-group and fork length in striped bass from the Roanoke River, North Carolina, during April and May 1958, 1960, and 1963*

[Values in parentheses are the numbers of specimens upon which the mean values are based. These numbers do not total 159 because the weight of 1 fish and the lengths of 12 fish were not recorded. Sixteen fish could not be aged]

Fork length (inches)	Age-group									
	IV	V	VI	VII	VIII	IX	X	XI	XII	XIII
17.0–17.9	282 (1)	–	–	–	–	–	–	–	–	–
18.0–18.9	222 (7)	231 (1)	–	–	–	–	–	–	–	–
19.0–19.9	332 (8)	–	345 (1)	–	–	–	–	–	–	–
20.0–20.9	341 (26)	409 (4)	289 (1)	–	–	–	–	–	–	–
21.0–21.9	385 (15)	363 (2)	–	–	–	–	–	–	–	–
22.0–22.9	402 (5)	413 (5)	616 (3)	–	518 (1)	–	–	–	–	–
23.0–23.9	–	522 (2)	570 (1)	548 (1)	524 (1)	–	476 (1)	–	–	–
24.0–24.9	642 (1)	878 (1)	684 (1)	512 (2)	812 (3)	–	–	–	–	–
25.0–25.9	–	–	902 (2)	749 (6)	933 (3)	833 (3)	–	–	–	–
26.0–26.9	–	–	–	848 (7)	577 (1)	887 (2)	903 (1)	–	–	–
27.0–27.9	–	–	–	783 (1)	976 (4)	977 (3)	863 (1)	815 (2)	–	908 (1)
28.0–28.9	–	–	–	–	729 (1)	988 (2)	1,082 (2)	–	1,136 (1)	–
29.0–29.9	–	–	–	–	–	825 (1)	1,055 (1)	1,199 (1)	–	–
30.0–30.9	–	–	–	–	–	–	–	1,029 (1)	–	–

TABLE 3.—*Estimated mean number of mature ova (thousands) by body weight and fork length in striped bass from the Roanoke River, North Carolina, during April and May 1958, 1960, and 1963*

[Values in parentheses are the numbers of specimens upon which the mean values are based. These numbers do not total 159 because the weight of 1 fish and the lengths of 12 fish were not recorded. Sixteen fish could not be aged]

Fork length (inches)	Body weight (pounds)													
	2.0–2.9	3.0–3.9	4.0–4.9	5.0–5.9	6.0–6.9	7.0–7.9	8.0–8.9	9.0–9.9	10.0–10.9	11.0–11.9	12.0–12.9	13.0–13.9	14.0–14.9	15.0–15.9
17.0–17.9	–	282 (1)	–	–	–	–	–	–	–	–	–	–	–	–
18.0–18.9	163 (3)	239 (4)	339 (1)	–	–	–	–	–	–	–	–	–	–	–
19.0–19.9	–	244 (4)	372 (6)	–	–	–	–	–	–	–	–	–	–	–
20.0–20.9	–	–	320 (23)	411 (10)	–	–	–	–	–	–	–	–	–	–
21.0–21.9	–	–	298 (2)	400 (15)	401 (1)	–	–	–	–	–	–	–	–	–
22.0–22.9	–	–	–	446 (3)	454 (8)	490 (3)	–	–	–	–	–	–	–	–
23.0–23.9	–	–	–	–	570 (1)	517 (4)	–	524 (1)	–	–	–	–	–	–
24.0–24.9	–	–	–	–	–	–	664 (6)	839 (2)	–	–	–	–	–	–
25.0–25.9	–	–	–	–	–	–	–	792 (7)	864 (7)	–	–	–	–	–
26.0–26.9	–	–	–	–	–	–	577 (1)	903 (1)	851 (8)	898 (1)	–	–	–	–
27.0–27.9	–	–	–	–	–	–	–	–	923 (3)	862 (4)	960 (5)	–	–	–
28.0–28.9	–	–	–	–	–	–	729 (1)	–	–	–	988 (2)	959 (2)	1,090 (2)	–
29.0–29.9	–	–	–	–	–	–	–	–	–	–	–	–	1,012 (2)	1,055 (1)
30.0–30.9	–	–	–	–	–	–	–	–	–	–	–	–	–	1,029 (1)

Chesapeake Bay, Jackson and Tiller (1952) found more eggs per pound of body weight in older fish than in younger ones. For every pound of body weight, ovaries from these fish contained from 62,000 to 112,000 eggs. Our study yielded a value of approximately 80,000.

We examined for curvilinearity the relation of total number of mature ova per fish to body weight, fork length, and age. The regressions of total number of mature ova on body weight and on fork length were linear.[1] Similarly, the number of mature ova as a function of age increased linearly to age-group IX, then began to curve. Subsequent analysis was limited to the linear data. The regressions for each feature did not differ significantly among the 3 years; therefore, the data for each relation were pooled.

We also examined the data to determine which relationship had the least variability. In general, the coefficient of variation of any sample estimate is equal to the standard error of estimate divided by the value being estimated and, accordingly, is a measure of relative variation. In a bivariate distribution, $f(x, y)$, the coefficient of variation of the regression of Y on X is

$$\text{CV}\ (b)\ = \frac{\sqrt{s^2/\Sigma x^2}}{b},$$

where: $s^2 = \dfrac{\Sigma y^2 - b\,\Sigma\, xy}{n-2}$ and b is the estimated regression coefficient.

Comparison of these coefficients for the regressions of egg number on age, length, and weight, viz.,

$$\text{CV}\ (b)\ \text{age} = 0.0604$$

$$\text{CV}\ (b)\ \text{length} = 0.0414, \text{ and}$$

$$\text{CV}\ (b)\ \text{weight} = 0.0366,$$

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[1] The apparent straight-line relationship between ova number (a volume function) and fish length (a linear function) would appear questionable. Among the specimens examined, however, variability of the measurement data masked expected curvilinearity and therefore prompted our use of the simpler linear regression technique.

indicated that of the three suggested predictors, weight had associated with it the least amount of variability. For prediction we therefore computed a simple linear regression of egg count (Y) on weight (X) (Figure 1). The equation for estimating number of ova ($\hat{Y}$) is:

$$\hat{Y} = \bar{y} + b(X - \bar{x}) = 555{,}182 + 75{,}858(X - 7.3)$$

and the 95% confidence interval for the mean egg count of all fish at a given weight (X) is:

$$\text{CI } (\hat{Y}) = \hat{Y} \pm 24.19\sqrt{0.0063 + \frac{(X - 7.3)^2}{1{,}770}} .$$

This relationship, in conjunction with measures of population size and sex ratio, permits estimation of the approximate number of mature ova that a spawning population can produce.

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What We Know About Shrimp Size and the Tortugas Fishery[1]

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SEVERAL MONTHS AGO I was asked if I would give a paper today entitled "It pays (or it does not pay) to catch small shrimp in the Tortugas shrimp fishery." But what do you do when you are on the horns of a dilemma? At the time, I was on those horns, so after thinking a bit I replied that I'd give a paper on "What we know about shrimp size and the Tortugas fishery." I thought this subject was innocent enough because we had a mark-recapture experiment going which I was sure would provide answers. I didn't know it was going to take so long to get the answers, though.

Before tackling the yield curves the computer coughed up, I think we should

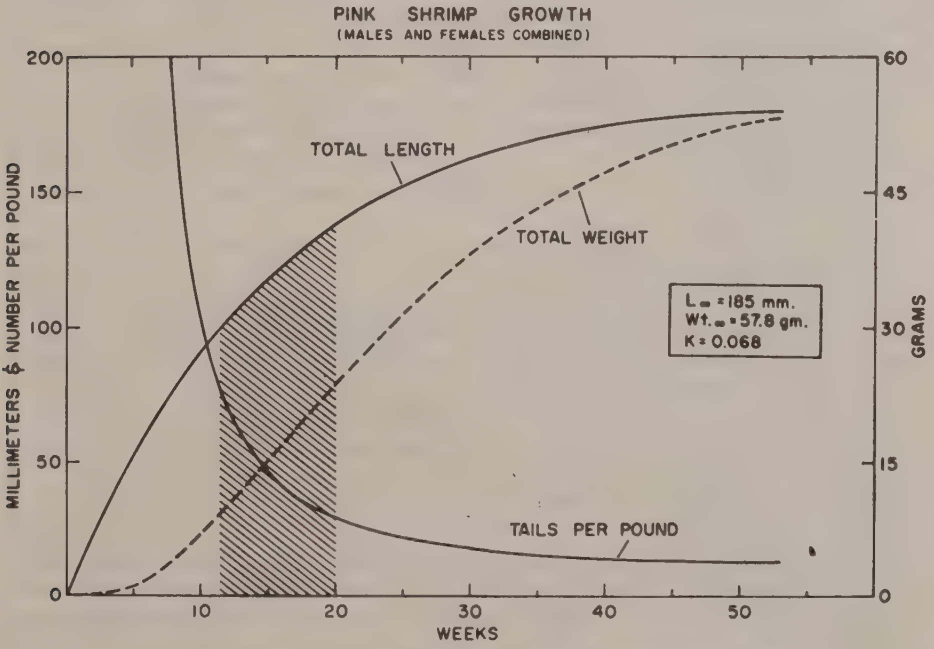

FIG. 1. Growth of Tortugas pink shrimp determined from mark-recapture experiments.

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[1] Contribution No. 214, Bureau of Commercial Fisheries Biological Laboratory, Galveston, Texas.

have an understanding of how Tortugas pink shrimp grow in relation to time.

Fig. 1 shows the growth of pink shrimp on the Tortugas shrimping grounds. Like much of the data I shall present, this graph is based on mark-recapture experiments and represents our latest approximation. We have combined males and females and have used the Von Bertalanffy growth equation since it seems to fit our data well.

Time, in weeks, is given along the horizontal axis. As we proceed from left to right, the first ascending curve shows increase in length with time and the next ascending curve, increase in weight with time. The descending curve shows the count of shrimp in tails-per-pound with time. The figures in the box on the right—185 mm, 57.8 grams, and 0.068—represent the constants used in calculating the total length and total weight curves. The shaded area covers the portion under discussion today.

I think this illustration is most revealing in that it demonstrates the rapidity with which action takes place in the growth of pink shrimp and the short period of time and slight increment in length with which we are dealing.

If we consider 100 mm (4 inches) total length or 80 count tails as the size at which the shrimp are fully subject to fishing, we find that within about 9 weeks they have increased about 1½ inches in length and their weight has increased to where they are about 30 count. With these facts in mind, I think we can better understand that which follows.

Using these growth curves, Dick Berry of our staff has made an analysis of the size composition of the commercial landings from the Tortugas grounds from 1956 through 1964. This analysis reveals that a total instantaneous mortality of about 0.25 per week best describes the size distributions of the landings. On a percentage basis, about 22% of the shrimp are removed from the population each week by a combination of fishing and natural deaths.

Carefully designed and controlled mark-recapture experiments by staff members, Costello and Allen, and Berry and Knight, suggest that the instantaneous natural-mortality rate on the Tortugas grounds probably lies between 0.075 and 0.125 weekly. In other words, the natural mortality rate is between about 7 and 12% a week.

We have used these figures to construct some yield curves. Fig. 2 demonstrates the relative yield in weight that could be expected from a brood of shrimp that entered the fishery at 80 count tails-per-pound. In these two curves, which represent what we now think are the extremes, we have used the growth rate I just mentioned and a total instantaneous mortality of 0.25. The lower curve was developed by taking fishing and natural mortality each at 0.125 and the upper curve with a natural of 0.075, and a fishing of 0.175. For those of you who are interested, we did not use the Beverton and Holt (1957) formula but that of Thompson and Bell (1934) with a time interval of 1 day. The formulas are essentially the same, but the integrated formula of Beverton and Holt does not offer a ready means for the addition of price, which we needed. To put it simply, what we have done is to tie together growth, natural mortality, and fishing mortality to come up with some curves that show the tail count shrimp should reach before fishing begins in order to get the greatest poundage out of a brood.

In Fig. 2, the horizontal axis is in units of headless shrimp per pound and the vertical axis is in relative yield.

The lower curve tells us that if the rates used were the true rates, we would catch as many pounds of shrimp if we started fishing them when they were first fully recruited at 80 count to the pound, as we would if we waited until they grew to 60 count size.

The upper curve tells us that if the rates used were the true ones, we would catch the most pounds of shrimp if we did not start fishing until they reached 60 count, and we would still catch about the same number of pounds if we waited until they grew to 40 count. This is now what we believe to be our ballpark. The bounds lie somewhere between 80 and 40 tail count for maximum weight.

Note how the curves are broad-topped, rise slowly to a maximum, and decline rather abruptly thereafter. They indicate that though maximum weight may be obtained by starting to fish between 80 and 40 count, the safest size for maximum weight is about 60 count.

Now let's take a look at what happens when we add price as another factor. Fig. 3 shows the same two curves with price added. We now are considering

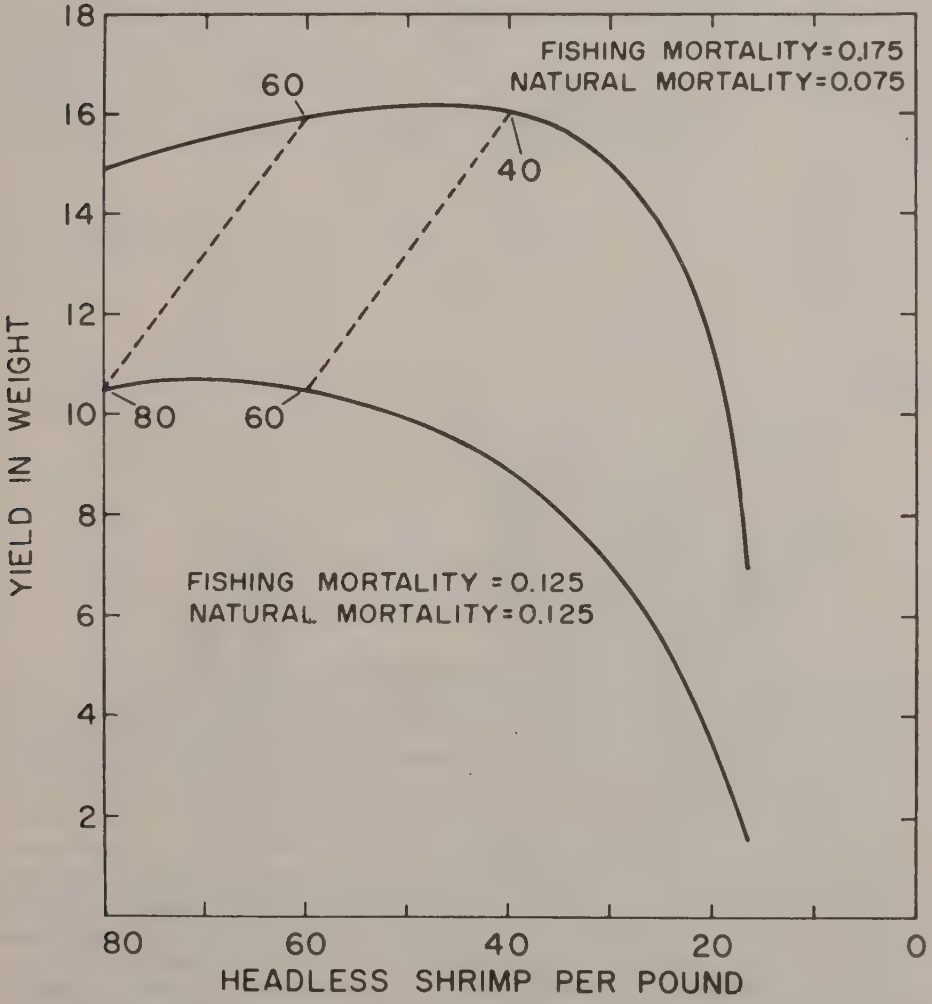

FIG. 2. Yield in weight curves for Tortugas pink shrimp.

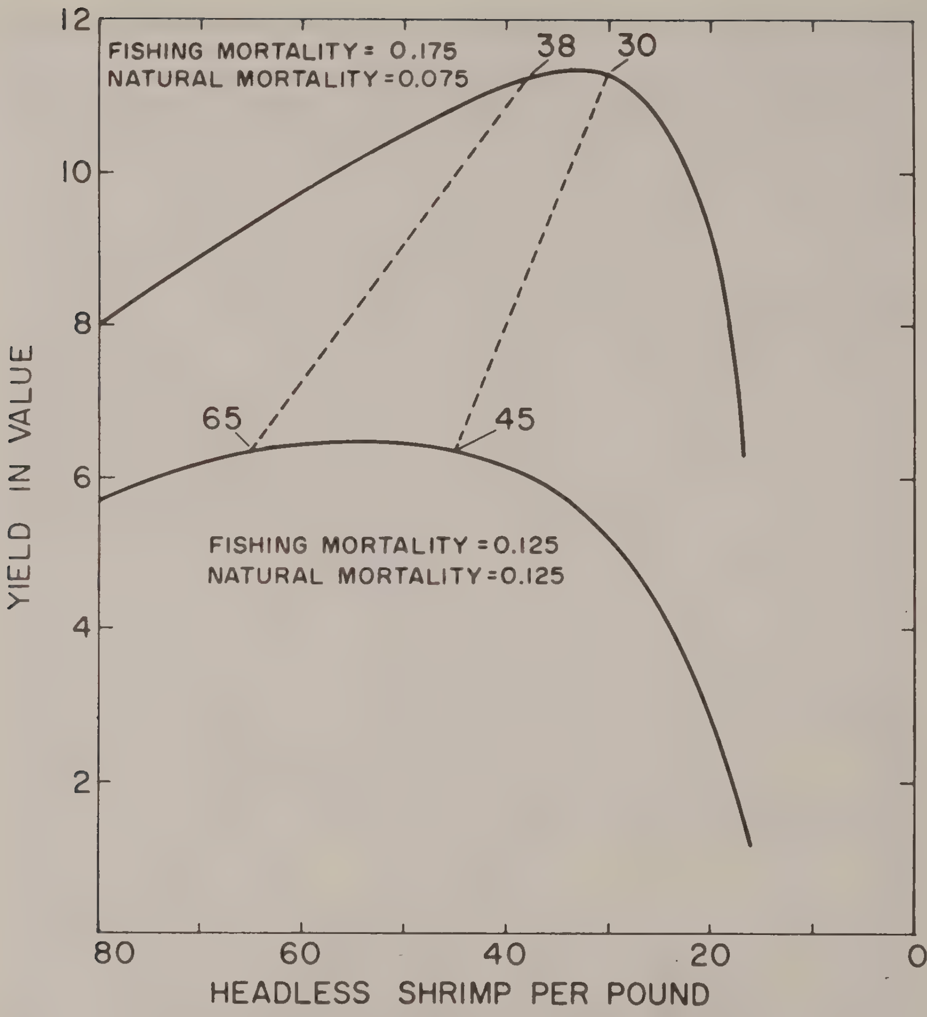

FIG. 3. Yield in value curves for Tortugas pink shrimp.

growth, natural mortality, fishing mortality, and price paid the fishermen. The prices we used for these curves ranged from 21.5 cents a pound for 70 and over count to 86 cents a pound for under 15 count. A break in price was made for each 5-count change in size. For example, 21-25 count shrimp were valued at 76 cents a pound, 26-30 count at 71 cents, and 31-35 count at 65 cents.

You will notice that when we take price into account, the curves shift to the right or toward a larger size shrimp for maximum value against a smaller size for maximum weight. The same growth, fishing, and natural mortality rates that gave a maximum weight of between 80 and 60 count give a maximum value between 65 and 45 count. At the other extreme, the maximum changes from between 60 and 40 count for weight to between 38 and 30 count for value.

This information looks good. We have now considered growth, natural mortality, fishing mortality, and price. It isn't complete, however. We lack

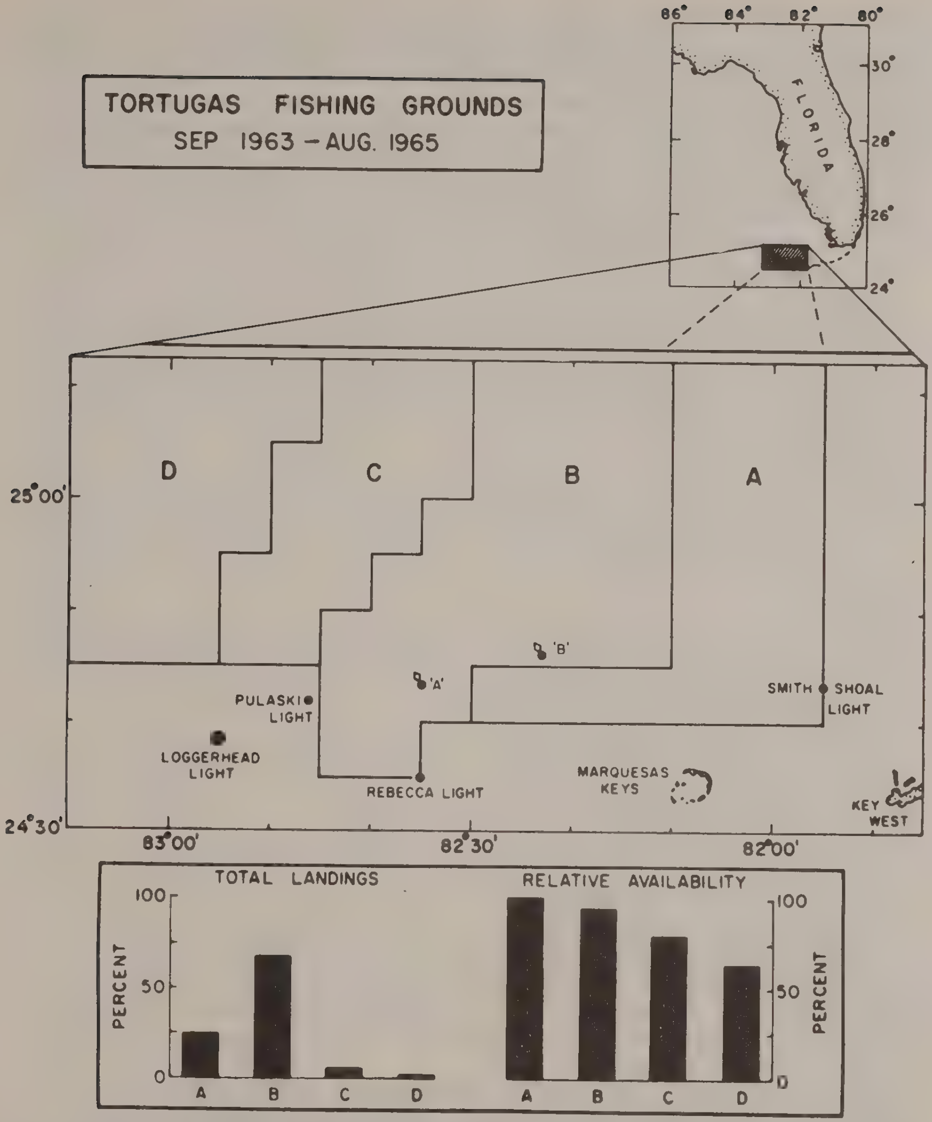

FIG. 4. Total landings and relative availability of pink shrimp from four fishing zones on the Tortugas fishing grounds. Zone depths in fathoms are: A, 9-12; B, 13-18; C, 19-23; and D, 24-30.

something. We lack fishing cost. We haven't entered fishing cost into our curves because, as yet, we have no good measure of it. For lack of a better term, I shall use "maximum profit" to indicate the situation when growth, natural mortality, fishing mortality, price paid the fishermen, and fishing cost are all taken into consideration.

When fishing cost is added, we think we know the direction the curves will shift, but we don't know the extent of the shift. We believe for the Tortugas fishery that when fishing cost is added to the value curves, maximum profit will lie to the left of maximum value. This shift means that the size at which fishing should begin to obtain maximum profit from a brood of shrimp will be less (a larger count size) than the size that will give maximum value. For example, let's say to get maximum value, fishing should be delayed until shrimp reach 40 count; then, to get maximum profit, fishing should not be delayed so long. For maximum profit, perhaps fishing should start at 50 or 60 count. We suspect when it is developed, that the count size for maximum profit will lie somewhere between the sizes for maximum value and maximum weight. Why do we suspect this? I think Fig. 4 will explain this.

Before discussing this figure, I want to make a flat statement to which I think most will agree. Fishing cost, or the cost of catching a pound of shrimp, is bound to be closely associated with the pounds of shrimp caught per hour of fishing and with the distance one has to travel from port to the fishing grounds. Fishing cost, then, must be closely associated with shrimp availability and with travel time.

Now let's look at Fig. 4. Here we have divided the Tortugas fishing grounds into four zones. Zone A covers depths between about 9 and 12 fathoms; B, between 13 and 18 fathoms; C, between 19 and 23 fathoms; and D, between 24 and 30 fathoms. The data cover 2 years from September 1963 through August 1965.

The bar diagram at the lower left shows the average percentage landings from these zones. During these 2 years, about 25% of the landings originated in Zone A, about 68% in Zone B; 6% in Zone C, and 1% in Zone D.

The bar diagram at the lower right represents the relative availability of shrimp in these zones as judged by the total landings from each zone divided by the total hours fished in each zone. The height of the bars shows the comparative availability of shrimp in each zone. With Zone A equated to 100%, the relative availability in Zone B is 95%; in Zone C, 70%, and in Zone D, 64%. Thus, if 1 hour of fishing in Zone A would produce 100 pounds of shrimp, the same hour of fishing in Zone D would produce only 64 pounds.

We must remember though that these figures are based on landings and not catch. On the basis of catch, there would be an even greater disparity between Zones A and D because of culling. A greater proportion of small shrimp are caught in Zone A than in Zone D. As a consequence, a greater proportion of the catch in Zone A is discarded, thereby lowering the landings from this Zone to a greater degree than those from Zone D.

It seems evident from these data, that the grounds nearest the port of Key West produce more pounds of shrimp for each hour of fishing than do the most distant grounds. We also know that Zones A and B produce smaller shrimp than Zones C and D. Since availability and distance favor the areas where smaller shrimp occur, it is apparent that the element of cost also favors the area of smaller shrimp.

It is dangerous to attempt to predict what the outcome of a research problem may be before the research is done, but from a superficial examination it looks as though the slope of the cost line favoring small shrimp will be less than that of the price line favoring large shrimp. This difference would place the size at which to start fishing to get maximum profit somewhere between the sizes for maximum weight and maximum value.

Just for argument's sake and so that I can have something further to talk about, let's hypothesize that we eventually come up with information that tells us we should not start fishing until shrimp reach 60 count.

Our goal now becomes, no shrimp caught until they reach 60 tails to the pound. Shrimp of this size are about 110 mm or about 4½ inches in total length.

The problem now is: how can we best attain this goal?

Right at the start, we know from the studies of Ingle, Eldred, Jones, and Hutton (1959), those of Iversen, Jones, and Idyll (1960), and ours that, owing to the ranges in shrimp size distributions and availability on the fishing grounds, either we are going to have to compromise on this size or else we have to have a gear that will not catch shrimp smaller than about 4½ inches long. So let's examine the possibility of gear modification in order to reach our goal.

At least for once, I anticipated a problem before it arose, and a couple of years ago I put Dick Berry to work on mesh-selectivity studies. His results are not greatly different from some unpublished preliminary conclusions Bill Anderson and I reached about 30 years ago nor do they differ much from those of Regan, Idyll, and Iversen (1957). All show that some slight benefit might be gained by using a larger mesh in the trawls. But, when the mesh size is increased sufficiently to get a significant increase in size of shrimp that escape, too many large shrimp also escape. So fishing becomes a nonpaying proposition. Furthermore, for proper escapement, the chafing gear would have to be removed.

With some fishes, mesh selectivity seems to be the answer for controlling the size at which harvest should begin. In fish, however, I think you will find that the animal dealt with is considerably larger than our shrimp, and that there are several inches in the animal's length and girth with which to deal. In shrimp, where only about 1½ inches in total length means the difference between 80 and 30 tail count, it is understandable why the control of mesh size is not adequate for our purposes.

It doesn't appear as though we have an easy way out, such as that provided by selective gear. Nor does it appear that we will be able to attain a sharp cut-off point at 60 count or any other count that eventually may be decided upon. The habits of the shrimp and their size distribution on the fishing grounds preclude any sharp cut-off point. We will always catch some small pink shrimp. All we can hope for is to arrive at some compromise that will give us the most profitable approach toward approximating our goal—particularly because we have no evidence that present fishing practices are depleting the shrimp stocks. What we are after is to conduct our fishing in such a fashion that we are getting maximum profit.

Basically, fishing should be conducted in such a manner that the fishermen get the greatest dollar return from the stocks of shrimp for the least cost of fishing, while at the same time the total catch should be as near to the maximum weight as possible. This problem, by its very nature, probably requires a compromise position though it may not prove to be so. When all the facts are in, we may wind up concluding that maximum weight is about the same as maximum profit.

Now that I've got that off my chest, let's proceed to look at control by size limit. You now have in Florida a size limit set at 70 count tails-per-pound with a 5% permissibility for shrimp smaller than 70 count.

Let me ask you shrimp people a few questions.

Don't answer them! Just think about them!

1. Where can you fish shrimp and not catch more than 5% over 70 count?

2. How do your catches in these places compare with your catches in areas where you get more than 5% over 70 count?
3. Is a caught shrimp a dead shrimp?
4. Does the law create wasteful practices?
5. Is this law truly enforceable?
6. Is it accomplishing what you wanted it to accomplish?

After you think about these questions a while, I believe you will agree with me that you already know the answers, or at least enough of them to arrive at the conclusion that an out-and-out size limit does not meet your needs. Furthermore, since it forces the fishermen to cull their catches, it is causing a waste that should not be.

A size limit in itself reminds me of the fellow with an ingrown toenail who, instead of trying to heal it, cut his toe off. Here is a real all-or-nothing solution. Very few problems with a biological foundation can be solved by the all-or-nothing process. To get the most out of nature, one must compromise with her. Also, to obtain the cooperation of the fisherman, and no regulation will work successfully without his cooperation, the fisherman must be convinced that the regulation is for his benefit.

Let's now look at a closed-season approach to the problem. If there were a particular time of the year when undersized shrimp were extremely abundant on the fishing grounds and large shrimp were not abundant, it might prove profitable to establish a closed season during that time. Unfortunately, from about September to May, when undersized shrimp are most abundant, the fishing grounds are most productive of large shrimp. It is only between about June and August, when shrimp are scarce and little fishing occurs, that undersized shrimp are not present in abundance on the grounds.

If you will recall Fig. 1, that of growth and time, I think you will understand why this situation exists.

So, the idea of a closed season goes down the drain.

Up till now, it seems I've been telling you what you should not do. I suspect, if I continue in this vein, one of you, at any moment, will pop up and ask, "Well, Lindner, what should we do?"

Now that I've been asked the question, here goes! I have three recommendations:

1. Repeal your size-limit law. It is not accomplishing what you want, nor will such a law, in Florida or anywhere else in our shrimp fisheries, accomplish what is wanted. The size distributions of our shrimp on the fishing grounds are such that size limits cause more waste than benefit.

2. You are really not hurting very much, though you may think you are, so sit tight until something better comes along. There are times when doing nothing is better than doing the wrong thing. At the moment, I think you are better off doing nothing. By nothing I mean nothing more than repealing the size-limit law.

3. Explore in detail the shrimp size-depth-availability relations that exist on the Tortugas grounds to see if closed areas are advisable.

My first and second recommendations speak for themselves. The third probably should be expanded a bit. You undoubtedly have gathered from what I have already said that I think our problem now is one of determining maximum profit. I believe we already know broadly the requirements for maximum weight and maximum value, but for maximum profit, we have one specifically unanswered question.

This question is: is there an area, or are there areas, where we should not fish in order to get maximum profit?

Fishing for maximum profit, of course, carries with it the connotation of no culling of the catch. All shrimp caught should be brought in and sold.

This question, I believe, can be answered by carrying out my third recommendation.

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TIME AND INTENSITY OF SETTING OF THE OYSTER, CRASSOSTREA VIRGINICA, IN LONG ISLAND SOUND

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The literature on the propagation of oysters is extensive. It consists of hundreds of articles in numerous publications, many of which are obscure State and local reports of comparatively limited circulation. Articles on spawning and setting of the American or Eastern oyster, *Crassostrea virginica* Gmelin (until recently known as *Ostrea virginica*), constitute by far the larger portion of the literature dealing with this aspect of oyster biology.

It would be impossible to offer here a comprehensive review of this voluminous literature. Furthermore, such review is unnecessary because the majority of the articles on the propagation of oysters have been included by Baughman (1948) in his annotated bibliography. Korringa (1952) commented on many articles that appeared after Baughman's bibliography was published, and recently Galtsoff (1964) offered another comprehensive résumé. Thus, with the exception of a relatively few papers published during the last year or two, I shall mention principally the articles directly pertaining to the propagation of oysters in New England waters, especially in Long Island Sound, where most of the work reported in the present paper was done.

A general description of the Long Island Sound region has been given in several previous papers (Prytherch, 1929; Loosanoff and Engle, 1940; Loosanoff, 1964). It will therefore be sufficient merely to point out here that the oyster setting grounds in Long Island Sound are confined principally to the Connecticut side, where the outline of its shore is irregular, composed of numerous harbors, bays, and other indentations. Many streams and rivers enter the Sound on the Connecticut shore; some form extensive estuaries, as that of the Housatonic River.

Long Island Sound has been an extremely important area since the cultivation of oysters was begun in the United States. One of the best historical reviews of the Connecticut oyster fisheries was given by Sweet (1941). As early as 1845, seed oysters collected from natural beds were planted in other areas and, eventually, plantings of large quantities of seed oysters were made in deeper waters of Long Island Sound on grounds which normally did not produce these mollusks. The planting of old shells to catch oyster set was initiated along the Connecticut shore of Long Island Sound in 1847, 8 years before the famous French oyster expert, Coste, began his extensive and successful experiments on cultivation of oysters in France.

During the prosperous era of the Connecticut oyster industry, the cultivated beds extended in a strip three to five miles wide, from Stony Creek to Stamford, a distance of about 40 miles. At one time nearly 50,000 acres of bottom were under cultivation.

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According to the records of many Connecticut oyster companies, only a few of which still exist, and reports of the Connecticut Shellfish Commission, heavy oyster sets were routine during the last quarter of the 19th century (Loosanoff and Engle, 1940). Between 1904 and 1925, however, a period of 22 years, not a single heavy set occurred in the Sound. Since 1925, good sets have occurred in Long Island Sound in only a few years, namely, 1930, 1939, 1940, 1941, 1944, 1945, 1955, and 1958. The other years have been complete failures or so-called marginal years during which either the set was general but too light to be commercially important, or the set was good in some sections of the Sound but failed in the major portion of the oyster-producing area.

The method which Connecticut oyster farmers use to obtain new oyster generations consists of spreading on the oyster beds each summer large quantities of old shells to which metamorphosing larvae can attach. In some years, when the industry experienced periods of prosperity, over a million bushels of oyster shells were planted in areas where setting of oysters could be expected. Plantings extended from the mean low-water mark to a depth of 40 feet or sometimes deeper. When setting failed, the planting of shells resulted in heavy monetary losses.

Because of infrequent and generally light sets, the oyster industry began to feel the lack of seed oysters and looked for explanations for the failure of oysters to set in Connecticut waters. Furthermore, since the oystermen had no knowledge as to when the heaviest periods of setting might occur, they often planted shells either too early or too late to obtain the best sets, even during good years. This situation existed in the early 1920's, when the U. S. Bureau of Fisheries detailed an investigator to Connecticut to work on the problem of lack of set (Prytherch, 1929). The original and primary purpose of these studies was to determine, if possible, the presence of clear-cut relationships between successful propagation of oysters and the conditions of their environment and, on this basis, to develop methods for predicting well in advance the time and intensity of setting of oysters.

It was believed originally that not more than 5 to 7 years would be required to gather the necessary data. For several reasons, however, these investigations had to be continued over a much longer period; eventually they covered more than a quarter of a century. Within a few years after beginning these observations it was discovered that variations in time and intensity of oyster setting were not as simple to explain and predict as had been first thought (Prytherch, 1929). Moreover, in the early 1930's I began to issue special bulletins for the information of the oyster growers on gonad development, spawning and setting of oysters, and survival of oyster set. These bulletins became of considerable interest and value to the oystermen and they insisted on a continuation of this work. During these studies over 60 articles were published on various aspects of biology of oysters, several of which are referred to in this paper. Many others on improvement of methods of oyster cultivation and control of their enemies were also written. Some of the latter, for example, the observations on spawning and setting of the common starfish, *Asterias forbesi,* of Long Island Sound, have been published (Loosanoff, 1964).

All of the results of these investigations cannot be conveniently discussed in a relatively short paper. The present article, therefore, is devoted to a description of the chronological aspects of spawning and setting of oysters in Long Island Sound and is to be followed by two more on the numerous biological and ecological variables that affect the propagation of oysters. To be included in the later articles are statistical analyses of the data to evaluate their relative importance and their possible value in predicting some important aspects of spawning and setting.

The data in this article are based upon observations made at many stations, but chiefly those at a depth of 30 feet or less. Statistical analyses already reported (Loosanoff, 1964) have shown that conditions at stations located at 30 feet and less are representative for the entire Long Island Sound.

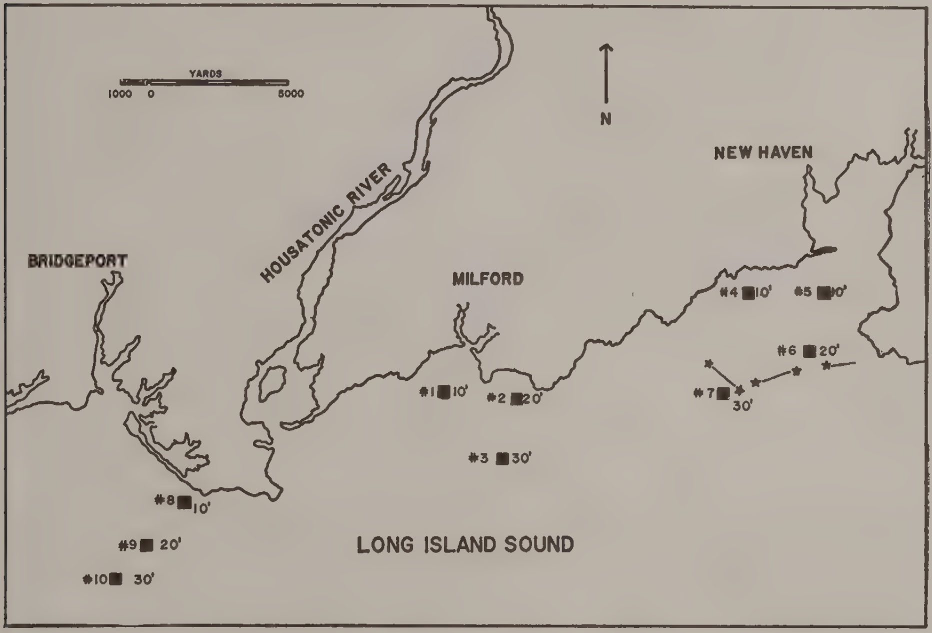

FIGURE 1. Location and depth of 10 stations established for observations on time and intensity of setting of oysters in Long Island Sound, 1944–61.

METHODS

These studies were conducted from 1937 to 1961 at the U. S. Bureau of Commercial Fisheries Biological Laboratory, Milford, Connecticut. In 1937–43 the chain of stations sometimes extended from Thimble Islands, east of Branford, to Westport (Loosanoff and Engle, 1940). In 1944–61 (except 1957, when only three stations were maintained), observations were carried on at the same 10 stations, located between New Haven and Bridgeport (Fig. 1). The studies dealt with various aspects of the propagation of oysters, including gonad development, discharge of spawn, occurrence and distribution of larvae, and the beginning and end of setting of larvae. The variations in time and intensity of setting throughout each summer constituted part of this investigation. Included also were systematic studies of environmental factors, among them changes in temperature, salinity, and pH of the water, amount of precipitation, river discharge, hours of sunshine, direction and velocity of winds.

The time and intensity of setting in different areas were determined by examining special collectors placed at each station. These devices (Fig. 2), which were wire bags filled with clean oyster shells, were first suggested in 1925 by Captain E. C. Wheeler of the Connecticut Oyster Farms Company. We have used this type of collector successfully in Virginia (Loosanoff, 1932), and later throughout the entire period of our studies in Connecticut.

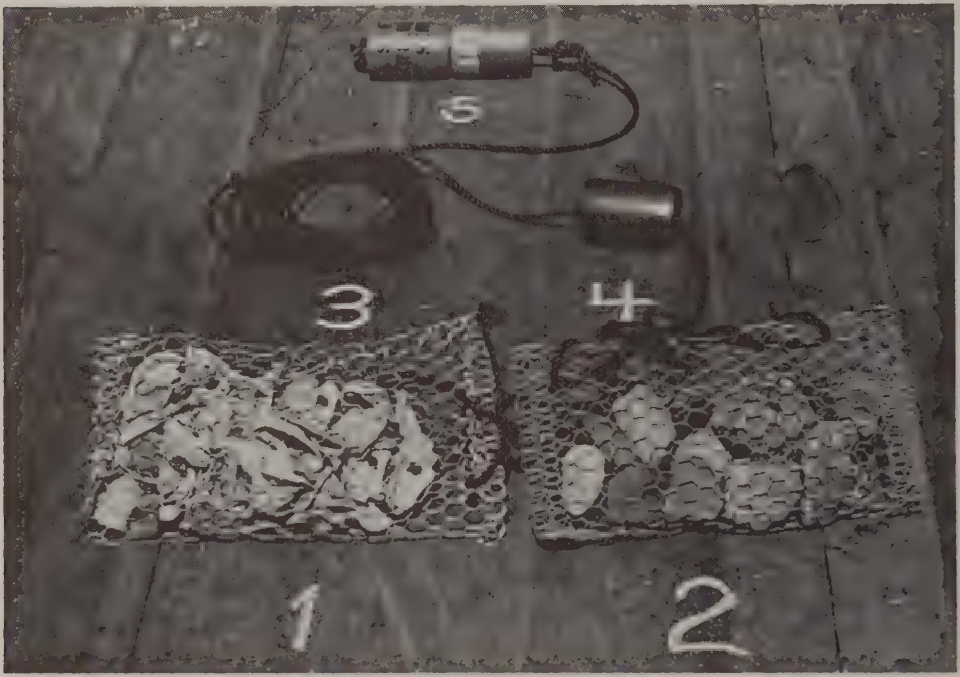

FIGURE 2. Type of collectors used for observations on setting of oysters in Long Island Sound. Description in text.

The wire-bag collector (Fig. 2-1) contained about 35 or 40 oyster shells of more or less uniform size. Two bags were used at each station. Another bag (Fig. 2-2), filled with small rocks, served as an anchor. A treated rope (Fig. 2-3) was run from the shell bags to the anchor bag, then to the auxiliary buoy (Fig. 2-4), which supported the middle portion of the rope, especially after it became waterlogged. A brightly colored buoy (Fig. 2-5) indicated the location of the collector.

Collectors were changed twice a week. The bags were brought into the laboratory and the shells examined within a few hours. The men counting the set were trained to distinguish oysters of different ages, from the time of attachment until they were about four days old. The set was counted on the inside surfaces of 20 shells taken at random from each collector and the results were later expressed as the number of oyster spat per 100 shell surfaces. This method is identical to the one used in studies of variations in time and intensity of starfish setting in Long Island Sound (Loosanoff, 1964).

Since two collecting bags were used to gather the data for each station and for each collection date, a pair of values was always available. It was possible, then, to correlate these values and to obtain an estimate of the reliability of the data. This analysis was made for two years, 1944 and 1955, which were chosen because the set of oysters was fairly heavy both years and because both years were characterized by considerable heterogeneity among the various stations. The only collection dates included in the analysis were those on which the set was appreciable, 10 or more oyster set in at least one of the 20 bags. For each date a correlation was computed between oyster set in bag A and oyster set in bag B from each of the 10 stations. These correlations ranged from 0.65 to 0.98 in 1944 and from 0.66 to 0.98 in 1955; the agreement between the two samples taken at the same time and place was excellent.

Observations

Systematic observations on gonad development and spawning of the oysters of Long Island Sound were conducted every summer from 1937 to 1956, a period of 20 years. A detailed description of gonad development has recently been given (Loosanoff, 1965).

In general, the spawning period in Long Island Sound waters lasts 2½ to 3 months; this time is considerably shorter than in warmer southern waters where, in some areas, spawning may continue throughout the greater part of the year (Hopkins, 1954). Prytherch (1929) offered a method which, in his opinion, was reliable enough to predict the start of spawning of oysters in Long Island Sound one month in advance. According to him a prediction could be made on the basis of several factors, of which water temperature from April to July was the most important. The strange part of Prytherch's proposal was the statement that the prediction could be made between July 1 and July 10 of each year, a period which obviously is too late for such a prediction because the spawning in Long Island Sound normally starts between June 26 and July 3 (Loosanoff, 1965).

Observations on occurrence and distribution of oyster larvae in the inshore waters of Long Island Sound constituted an integral part of this study. Unfortunately, they could not be carried out over as broad a scope as was desired, because of scarcity of personnel. Nevertheless, even these limited observations provided rich information of considerable biological interest.

Plankton samples for determination of the number of oyster larvae were collected by filtering known volumes of sea water through plankton nets. In our earlier studies, 50-gallon samples were pumped from near the surface and bottom, but because oyster larvae were rather uncommon, the volume of samples was later increased to 100 and eventually to 200 gallons. To facilitate the collection of such large samples the water was filtered through two nets: first, a coarser one made of #10 plankton netting, which retained most of the zooplankton, including larger bivalve larvae, and then through a #20, net, which retained the smaller larvae. The use of a #10 net prevented the clogging of the finer #20 mesh. This method is still used at Milford.

Several students of oyster propagation (Baughman, 1948) have made observations on the distribution of oyster larvae in Long Island Sound. In earlier articles, including Loosanoff and Engle (1940), many figures were based on the counts of younger, so-called straight-hinge stages of larvae. Since oyster larvae at that stage have an appearance almost identical to larvae of some other species, for example, those of *Mulinia lateralis,* these early counts were not wholly reliable.

Similar errors cannot be made, however, in identification of older oyster larvae, measuring 100 microns or more. The oyster larvae of this size are unique in appearance; no larvae of other bivalves of Long Island Sound can be mistaken for them, with the possible exception of larvae of *Teredo.* Even larvae of *Teredo* and oysters are sufficiently different to be distinguished by an experienced worker.

Since the studies on distribution and occurrence of oyster larvae covered more than 25 years, they are too extensive to be discussed in detail here. Only a brief summary of this subject is offered, therefore. In general, oyster larvae in Long Island Sound, especially those of advanced stages, were never numerous; they were unevenly distributed over the oyster-producing areas, and their appearance or disappearance did not follow any definite pattern.

Frequently the samples of larvae were composed entirely of individuals of advanced stage of approximately the same size. This observation was interpreted to mean that the larvae probably originated in an area other than the place they were collected and were brought along as advanced larvae with masses of water which retained their identity during the entire period of larval development.

Our efforts to correlate the numbers of larvae with some obvious factors of their environment were mostly unsuccessful. The literature contains several referances (including that of Nelson, 1925) in which unsuccessful setting of oysters is attributed to ctenophores that have, presumably, eaten the majority of the larvae originally present. During the studies we had many opportunities to test this theory. We found, however, that no clear-cut relation existed between the numbers of ctenophores and the failure of oyster set. For example, ctenophores were so numerous in the Bridgeport-New Haven area between July 28 and August 12, 1944, that swimming was discontinued at many beaches, and collection of plankton samples was practically impossible even though several straining devices were used to prevent the ctenophores from entering the nets. Yet, this period produced one of the heaviest oyster settings in the history of Connecticut oyster farming.

Neither could the numbers of larvae be correlated with the numbers of parent oysters living in Long Island Sound. For example, in 1937, when more than a million bushels of adult oysters were growing in the Sound, many plankton samples taken in the middle of summer contained no oyster larvae (Loosanoff and Engle, 1940). On the other hand, in 1958, when the adult oyster population was extremely small, oyster larvae, especially those in advanced stages, were numerous, sometimes as common as three mature larvae per gallon of water.

Dead or dying bivalve larvae were found in our samples during some summers. One such observation was made in 1959 at Stations 2 and 5 in New Haven Harbor. Samples collected on August 20 contained many living larvae that appeared abnormal. A few days later, on August 24 and especially August 31, many dead or dying larvae were taken.

Sufficient evidence is available to suggest that the absence or disappearance of the larvae from the waters of Long Island Sound may often be due to the plankton blooms that occur in this area in the summer. These blooms probably produce large quantities of external metabolites which are detrimental to larvae. It has been shown experimentally at our laboratory that a dense bloom of dinoflagellates causes abnormal development of eggs and larvae of the clam, *Mercenaria mercenaria,* and the oyster (Davis and Chanley, 1956). Even when eggs of oysters were placed in water from which the dinoflagellates were removed by a Millipore filter, the development of the eggs and larvae was still abnormal. It is also possible that during the periods of heavy blooms of dinoflagellates, such as *Prorocentrum triangulatum,* some nannoplanktonic forms, which constitute the food of oyster larvae, disappear and, as a result, the larvae may starve or grow slowly and be more susceptible to diseases.

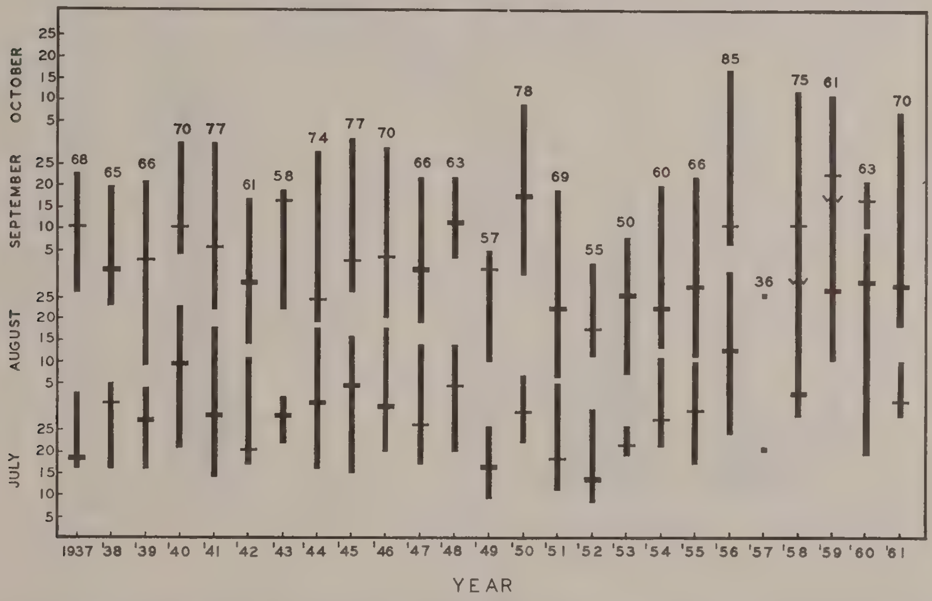

FIGURE 3. Beginning, end, and extent of setting period of oysters in different years in Long Island Sound, 1937–61. Cross-bars indicate the peaks of first and second waves of setting, the broader bars indicating the peaks of the heavier waves. Figures at top of each bar show number of days in setting period of each year.

The latest date at which mature larvae were found in our samples was October 8 (1959) when several were taken at Station 2, Milford Harbor, and 17 immature larvae were collected at Station 10 in Bridgeport Harbor.

In general, the length of the setting period of *C. virginica* increases from north to south. In Long Island Sound, as is shown later, this period extends from approximately the middle of July until the end of September or even early October.

Table I

Numbers of oyster set on 100 shell-surfaces, recorded semi-weekly at stations at 10 different depths off Stratford Point, Long Island Sound, 1939

Station number	1	2	3	4	5	6	7	8	9	10
Depth in feet	0	5	10	20	30	40	50	60	70	100
Date	Numbers of oyster set									
July 13	0	0	0	0	0	0	0	0	0	0
17	0	0	0	0	0	0	0	0	0	0
20	120	20	20	60	60	0	10	0	0	0
24	590	1030	960	630	290	160	30	50	0	0
27	21560	26560	9980	13690	29980	9630	1420	370	20	10
31	6760	14340	27260	30430	21830	10040	1100	840	110	160
Aug. 3	310	570	440	310	140	0	40	20	10	0
7	0	0	0	0	0	0	0	0	0	0
10	0	0	0	0	0	0	0	0	0	0
14	0	0	0	0	0	0	0	0	0	0
17	0	0	0	0	0	0	0	0	0	0
21	10	10	0	10	0	0	0	0	0	0
24	0	0	0	0	10	0	0	0	0	0
28	0	50	30	10	30	0	30	0	0	0
Sept. 1	0	0	0	20	20	10	0	0	0	0
4	20	20	40	190	480	10	30	10	0	0
7	100	60	40	200	200	30	0	0	0	0
11	40	30	10	40	70	40	0	0	0	0
14	0	30	30	10	0	0	10	0	0	0
19	10	0	10	20	0	0	0	0	0	0
21	10	10	0	0	0	0	0	0	0	0
25	0	0	0	0	0	0	0	0	0	0
28	0	0	0	0	0	0	0	0	0	0
Station total	29530	42730	38820	45620	53120	19920	2670	1290	140	170

In Chesapeake Bay it normally continues from the middle of June until the middle of October (Loosanoff, 1932; Beaven, 1954). In South Carolina, however, the season is considerably longer than at either of the northern points just mentioned; it extends from early May through a large part of October (McNulty, 1953). Finally, according to Hopkins (1954) larvae of *C. virginica* set from April until November along the Gulf of Mexico coast. Obviously, the length of the setting period depends upon the temperature; it is longer where the climate is warmer.

During the 25 years of observations in Connecticut waters, the beginning of setting varied from year to year between July 9 and August 11 (Fig. 3). The mean date was July 20, and in the majority of years first setting took place between July 16 and 22. This finding supports broadly the formula which was offered earlier by Loosanoff and Nomejko (1951) who stated (p. 124) that "The beginning of oyster setting in Long Island Sound should be usually expected on July 19 ±4 days, regardless of lunar phases and of changes in hydrostatic pressure caused by changes in the tidal level." The exceptions to the rule were the years of 1949, 1951, and 1952, when setting began between July 9 and 12, and 1959, the only year when the beginning of setting was recorded later than the end of July (Fig. 3).

The observations on setting of oysters were made in some years from the intertidal zone to the depth of 100 feet (Table I). Setting was recorded at all depths but, as with starfish (Loosanoff, 1964), the duration of the setting at the deepest stations was shorter than at the shallower ones.

As a rule, setting began at all the stations in 30 feet ot water or less within the

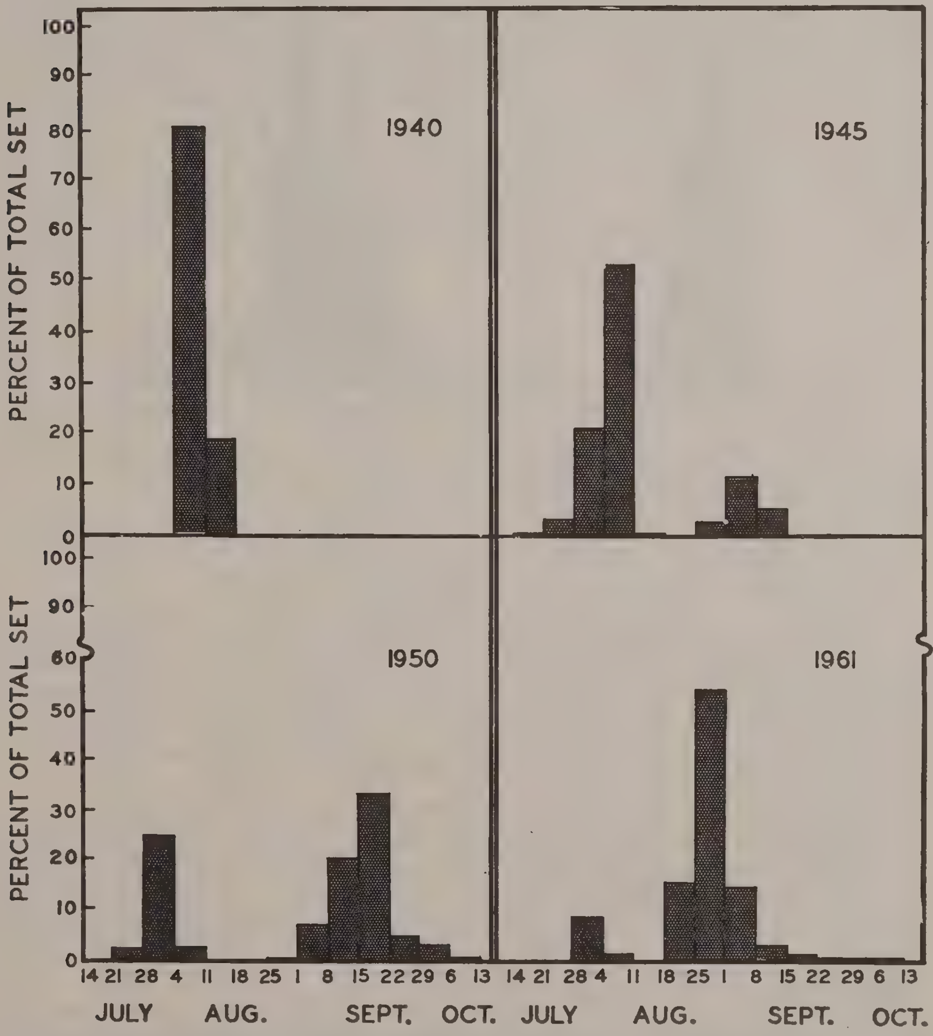

FIGURE 4. Variations in weekly intensity of oyster setting in different years. In 1940 99.76% of the entire set occurred within two weeks of the first wave, but in other years setting was more evenly distributed through the summer and two definite waves were distinguishable.

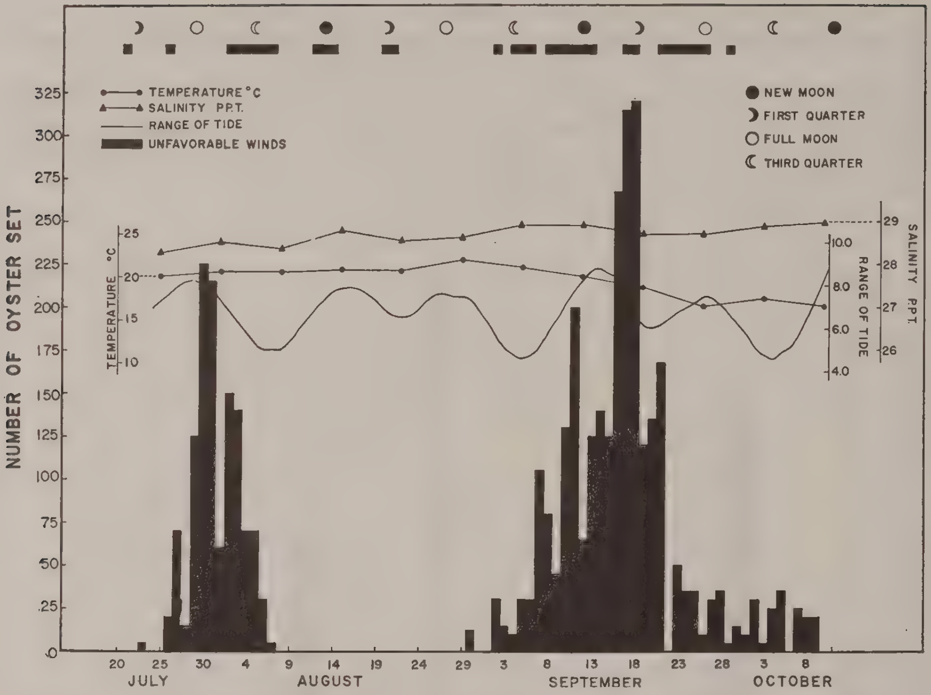

FIGURE 5. Average daily number of oyster set per station recorded in 100 oyster shell-surfaces in Long Island Sound, 1950. Two definite waves of setting, separated by a "dead period," can be seen. Some of the environmental conditions are also shown.

same 24-hour period. Even at stations located as deep as 50 or 60 feet, setting started at approximately the same time as at shallower stations.

As found in a parallel study on propagation of another invertebrate of Long Island Sound, the starfish (Loosanoff, 1964), the length of the setting period of oysters varied greatly in different years (Fig. 3). The shortest time between the beginning and end of setting was in 1957, only 36 days; while the setting period of the preceding year, 1956, extended for 85 days. In nine years the duration of setting was 70 days or longer, and the average length of the setting period was 65 days, or about two months.

The earliest date for the end of setting was August 26, 1957. This year, as mentioned earlier, had the shortest setting period. The latest date was October 17, 1956, when the period of setting was the longest within the period of our studies. The mean date for the end of setting was September 22. The difference between the earliest and the latest dates for the end of setting was 51 days, considerably larger than the difference of 34 days for the earliest and latest dates of the beginning of setting.

Although the average setting period of Long Island Sound oysters was about 65 days, the average length of the setting period of starfish during the same period was about 52 days. Thus, the lengths of the setting periods of these two invertebrates living under identical conditions do not differ radically.

The length of the setting period of oysters given here merely shows the number of days between the beginning and the end of setting. It does not mean that setting was continuous or of uniform intensity during this entire period. In reality, setting ceased for various (sometimes lengthy) periods almost every year. Such a "dead period," for example, occurred in 1950 when not a single oyster larva set on any of our collectors between August 7 and 30 (Fig. 5). This gap appeared even though the number of mature oysters in Long Island Sound then amounted to many millions. During most of this period the water of the Sound was colored somewhat pinkish by plankton blooms. A dinoflagellate, *Prorocentrum triangulatum,* was one of the common organisms present. In 1957 setting was recorded only on the first day and then 36 days later on the last day, while between these dates no setting occurred. The years 1958 and 1959 were exceptional because setting was continuous during practically the entire season (Fig. 3).

Further differences and peculiarities of setting in different years are illustrated in Figure 4. For example, the setting season extended for 70 days in 1940, but over 99% of the set was between August 5 and 18; the additional fraction of about 1% was spread so thinly through the remainder of the setting season that it cannot even be clearly shown in the illustration. Thus, during that year almost the

TABLE II

Average numbers of total oyster set per station per 100 shell-surfaces, and numbers of set recorded during each of the two waves, Long Island Sound, 1937–61

Year	Total set	Total 1st wave	Total 2d wave
1937	1640	1621	19
1938	1090	83	1007
1939	42623	42230	393
1940	42407	42378	29
1941	17225	15192	2033
1942	2138	71	2067
1943	72	57	15
1944	11147	10407	740
1945	4476	3530	946
1946	3267	1851	1416
1947	1136	438	698
1948	344	151	193
1949	739	730	9
1950	405	121	284
1951	1181	170	1011
1952	998	684	314
1953	2338	102	2236
1954	77	24	53
1955	10915	386	10529
1956	2289	1884	405
1957*	3	0	0
1958	15417	13903	1514
1959	2312	2250	62
1960	780	702	78
1961	234	23	211

* Only stations 1, 2, and 3, all in the Milford area, were maintained in 1957.

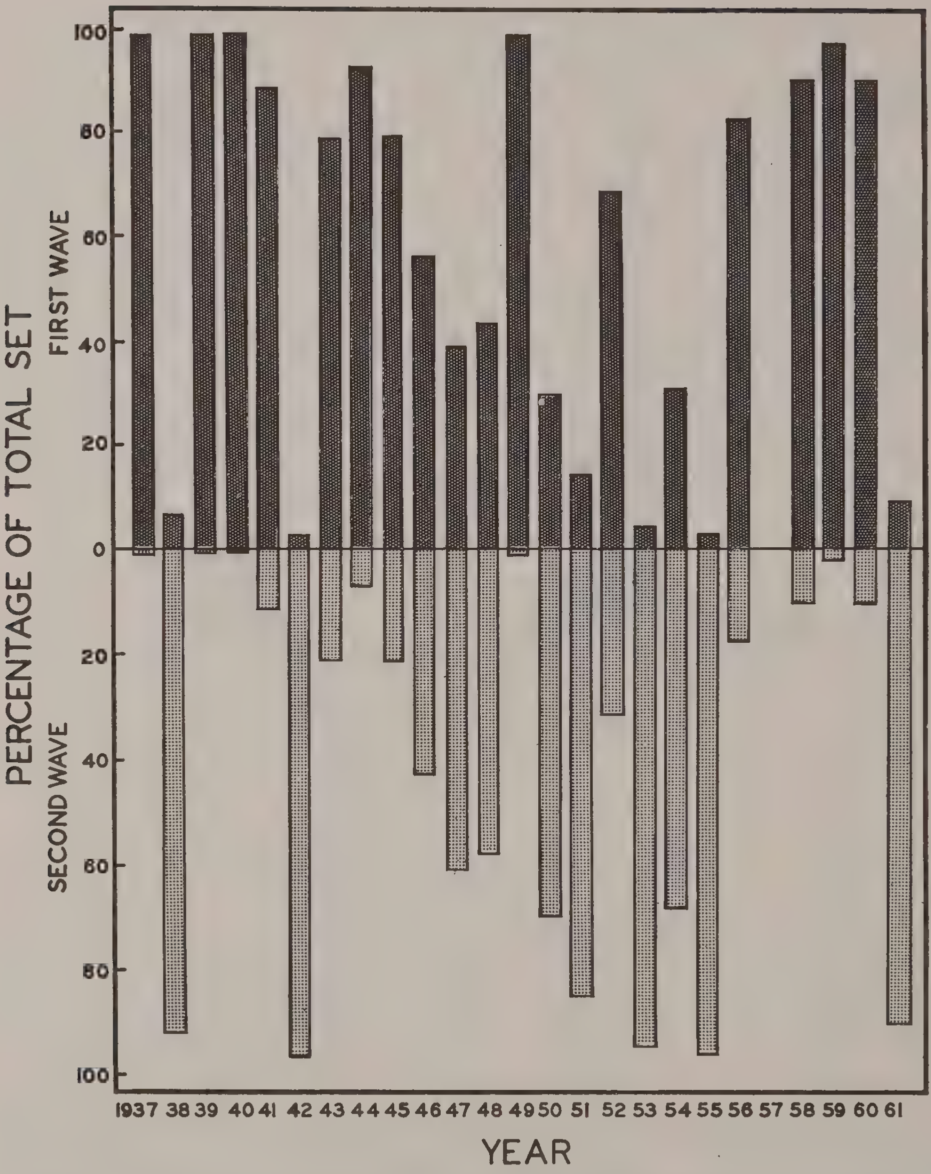

FIGURE 6. Percentage of total oyster set in each of the two waves during different summers, Long Island Sound, 1937–61.

entire setting occurred in a single wave of short duration. In 1945, however, setting took place in two waves, of which the first was the heavier. In contrast, during 1950 and 1961 the first wave of setting was the lighter of the two and the intensity of setting was much more evenly distributed throughout the setting period than in 1940 (Fig. 4).

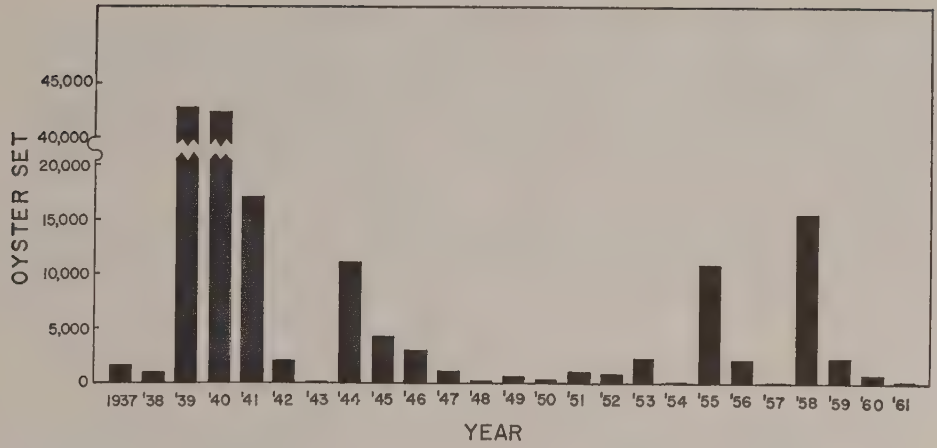

FIGURE 7. Average number of oyster set per station recorded in different years on 100 oyster shell-surfaces, Long Island Sound, 1937–61.

TABLE III

Average number of oyster set per station in different years on 100 oyster shell-surfaces, at stations located at 10-, 20-, and 30-foot depths, Long Island Sound, 1937–61

Year	Depth in feet		
	10	20	30
1937	2050	2175	695
1938	245	935	2090
1939	23945	45925	58000
1940	24635	54845	28200
1941	11454	21212	18515
1942	1000	2093	3345
1943	65	81	35
1944	24700	1775	2447
1945	6348	4649	1774
1946	1748	6508	2053
1947	1109	1467	842
1948	314	542	184
1949	783	585	833
1950	278	540	440
1951	848	707	2098
1952	1395	1283	183
1953	615	3028	3945
1954	74	95	63
1955	3660	7031	24473
1956	1641	1983	3457
1957*	5	5	0
1958	12977	32581	1505
1959	2216	3723	1030
1960	612	1376	406
1961	391	240	20

* Only stations 1, 2, and 3, all in the Milford area, were maintained in 1957.

Again we see a similarity in some aspects of setting of oysters and starfish of Long Island Sound because the latter also show considerable variation in intensity of setting during different summers. Sometimes the entire set may occur within a single week or 10 days, whereas in other years setting continues for a long time although the intensity may vary greatly from week to week (Loosanoff, 1964).

The beginning of the first wave of oyster setting varied from July 9 (1952) to August 11 (1959), and had a mean of approximately July 20 (Fig. 3). The earliest end of the first wave was July 21 (1957), a year of extremely poor setting, and the latest was September 17 (1959); the mean was approximately August 12. The date of the beginning of the second wave varied from August 7 (1951) to September 18 (1959), and the average was August 23; the end of the second wave which, of course, was the end of the setting season, came between August 26 (1957) and October 17 (1956); the average was about September 23.

TABLE IV

Rank-order of years in relation to the intensity of setting of oysters at stations of three different depths, Long Island Sound, 1937–61

Year	Rank-order of years at each depth (feet)				Year	Rank-order of years at each depth (feet)			
	10	20	30	All stations		10	20	30	All stations
1937	9	10	17	13	1950	21	21	18	20
1938	22	17	10	16	1951	15	18	9	14
1939	3	2	1	1	1952	12	16	21	17
1940	2	1	2	2	1953	17	9	5	9
1941	5	4	4	3	1954	23	23	22	23
1942	14	11	7	12	1955	7	5	3	6
1943	24	24	24	24	1956	11	12	6	11
1944	1	13	8	5	1957*	25	25	25	25
1945	6	7	12	7	1958	4	3	13	4
1946	10	6	11	8	1959	8	8	14	10
1947	13	14	15	15	1960	18	15	19	18
1948	20	20	20	21	1961	19	22	23	22
1949	16	19	16	19					

* Only stations 1, 2, and 3, all in the Milford area, were maintained in 1957.

The peaks, or maxima, of the waves also varied considerably from year to year. Their approximate dates are indicated in Figure 3 by cross-bars. The peaks of the first wave came between July 14 (1952) and August 29 (1960); the approximate average was July 30. The second wave had peak dates from August 19 (1952) to September 23 (1959), and an average of September 4. The difference in days between the maxima of the two waves ranged from 19 days (1960) to 40 days (1943).

Neither the first nor the second wave of setting was consistently the predominant one. Table II, giving average numbers of total oyster set per station for the two waves in each year, shows that each wave was dominant in a number of years. In some years almost 100% of the annual set took place during the first wave, but in others most setting was later in the season, during the second wave (Fig. 6).

Within the 25-year period the first wave was the heavier in 15 years and the second in 10.

In most years the heavier of the two waves predominated decidedly. Nevertheless, there were few years when the percentage of total set during the season was more or less evenly divided between the two waves. The years 1946, 1947, and 1948, when about a 40:60 ratio existed, were closest to such even distribution (Fig. 6).

The intensity of setting differed considerably from year to year. It was lowest in 1957, when only about three oysters per 100 shells were counted at each station during the entire season; in 1939 and 1940 over 42,000 spat were counted under identical conditions (Fig. 7, Table II). A comparison of the numbers of oyster set at the stations of the three different depths showed that no one depth consistently produced the heaviest set (Table III).

Each group of stations, whether at the 10-, 20-, or 30-foot depth, occupied the first, second, or third rank during one or more years of our observations. If all stations, regardless of depth, were considered, then, as already mentioned, 1939 was the year of heaviest setting, and 1957 was the poorest. Stations of different depths differed in this respect, however. For example, in 1939 the stations at the 30-foot depth had the heaviest set of the entire 25-year period (Table IV). For the 10-foot stations, however, 1939 ranked third, and for the 20-foot stations it ranked second.

In some other years the differences in intensity of setting at stations of different depths varied even more. Thus, 1944 was the best year for the stations at 10-foot depth, but for 20-foot stations it ranked 13th and for the 30-foot stations, 8th. For all the stations taken together regardless of their depth it ranked the 5th heaviest year in 25. In some years, nevertheless, as in 1943, the annual rank-order was the same at three different depths (Table IV).

I wish to thank my associates at the Milford Biological Laboratory who helped in collection of the data on which this article is based—especially my former biological aides, Charles Nomejko, John Malarkey, and James B. Engle, who examined the spat collectors. Joseph F. Lucash and Herman R. Glas captained the research boats. Mrs. Susan Webb prepared the illustrations and otherwise helped in completion of the manuscript. Harry C. Davis examined plankton samples collected during the last few years of these studies. Dr. Ralph Hile, Mr. Davis, and Miss Rita Riccio made helpful editorial suggestions.

SUMMARY

1. Studies on setting of oysters in Long Island Sound during a 25-year period, 1937–61, have shown that the larvae of advanced stages were never extremely common and were unevenly distributed in the water masses. Their appearance and disappearance did not follow a definite pattern.

2. No clear relation was found between the number of certain larval enemies, such as ctenophores, and intensity of setting. Neither could the numbers of larvae be correlated with the numbers of adult oysters.

3. Dead or dying larvae were sometimes found in plankton. Disappearance of the larvae possibly may be due to the plankton blooms that produce detrimental external metabolites. A dinoflagellate, *Prorocentrum triangulatum,* on occasion present in extremely large numbers, may be one of the forms responsible for the absence of larvae during certain periods.

4. Setting of oyster larvae was recorded at all depths from the intertidal zone to 100 feet.

5. Beginning of setting at all stations at the depth of 30 feet or less normally occurred within the same 24-hour period.

6. The average length of setting season of oysters in Long Island Sound was 65 days. The shortest season was 36 days, and the longest was 85 days.

7. Setting in different years started between July 9 and August 11; the mean date was about July 20. The earliest end of setting was August 26, and the latest, October 17.

8. The setting in Long Island Sound is not continuous or of uniform intensity. Setting ceased almost every year for various periods, sometimes several weeks long.

9. Setting exhibited two well-defined waves in most years; each peak had a clearly evident maximum. The time these peaks appeared varied considerably from year to year. The time between the peaks of two waves in different years ranged from 19 to 40 days.

10. Neither the first nor second wave of setting was consistently predominant. Within the 25-year period the first wave was the heavier in 15 years, and the second in 10.

11. The intensity of setting in the same areas of Long Island Sound differed widely from year to year. Setting was lowest in 1957, when approximately three recently set oysters per 100 shell-surfaces were counted at each station during the entire season; in 1939 and 1940 over 42,000 spat were counted under the same conditions.

12. Comparison of the numbers of oyster set at stations of three depths—10-, 20-, and 30-feet—showed that no depth consistently produced the heaviest set. Stations of each of the three depths had the greatest abundance of larvae during one or more years of the period of observations.

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DIMENSIONS AND SHAPES OF LARVAE OF SOME MARINE BIVALVE MOLLUSKS

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ABSTRACT

Recent development of methods of rearing bivalve larvae under controlled conditions has made it possible to culture the following species: *Arca transversa, Mytilus edulis, Modiolus demissus, Anomia simplex, Aequipecten irradians, Ostrea edulis, Ostrea lurida, Crassostrea virginica, Crassostrea gigas, Mercenaria* (=*Venus*) *mercenaria, Mercenaria* (=*Venus*) *campechiensis, Mulinia lateralis, Tapes semidecussata, Pitar* (=*Callocardia*) *morrhuana, Petricola pholadiformis, Ensis directus, Mactra* (=*Spisula*) *solidissima, Mya arenaria, Teredo navilis, Laevicardium mortoni*. These forms were grown past metamorphosis from eggs or recently released larvae of known parents. A series of photomicrographs and length-width measurements of larvae, from early straight-hinge stage to metamorphosis, is given for each species. In addition to these criteria, general shapes, prominence of the umbones and other morphological characters of the larval shells during growth are described. Problems and difficulties in identification, especially of closely related forms, are discussed, and suggestions for improved methods of identification are offered.

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INTRODUCTION

A student of zooplankton of estuarine areas is usually impressed with the high percentage of larvae of bivalve mollusks, as compared to the numbers of larvae of other invertebrates. Extensive data illustrating this preponderance are given in the work of Thorson (1946) on reproduction and larval development of Danish marine bottom invertebrates. Thorson found that approximately 58% of the total number of larvae in water samples during the 3-year period of his studies were those of lamellibranchs. These larvae were normally dominant during the summer and winter maxima, far outnumbering the larvae of echinoderms, polychaetes, prosobranchs and other groups. Similar observations have been made in many other areas but, in spite of the common occurrence of bivalve larvae in estuarine waters, their taxonomic identity remains uncertain. It is often impossible to place a larva taken in plankton in a definite species, genus, or even family.

Because of the lack of knowledge of the larval stages, we cannot become familiar with the complete life histories of many pelecypods. Moreover, it is now generally recognized that identification of different bivalve larvae from natural waters ceases to be a matter of only academic curiosity. The complexity of modern society, its technological progress, and the reflection of this progress upon marine and especially estuarine environments, create many problems in which our ability to tell larvae apart may be important. This is especially true in studies of pollution of water basins with industrial wastes or improperly used pesticides. For example, if we can distinguish larvae of different species, we can learn, from examination of plankton samples taken from an area the degree of pollution of which is known, what larvae can exist under that condition. Moreover, plankton samples taken just before and after the use of pesticides in the vicinity of or over certain bodies of water permit us to determine accurately the species of larvae that disappeared after the treatment. Finally, by collecting water samples at definite intervals after the applications of pesticides, analyzing them for the presence of pollutants, and examining and counting the larvae of different species, we may ascertain the cumulative effects of the chemicals on the various organisms.

Similar opportunities would be open for the studies, under natural conditions, of the effects on larvae of changes in turbidity, drastic reductions in salinity and unusually severe physical disturbances of the water during storms and hurricanes. In the same manner we should be able to estimate the effects of biological phenomena, such as water blooms which, by producing heavy concentrations of external metabolites, may kill the larvae of some species without affecting those of the others. In Long Island Sound we have often observed well-defined periods when oyster larvae practically disappeared during dinoflagellate

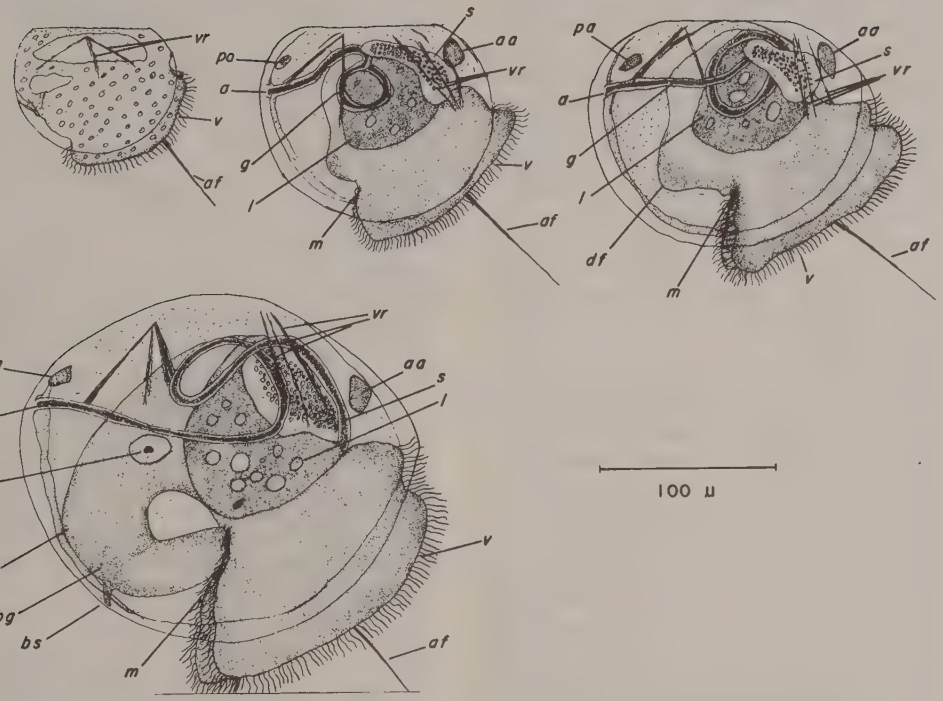


FIG. 1. Diagram of the prominent anatomical features of the larvae of the razor clam, *Ensis directus*, during different stages of development, from the first, shelled, straight-hinge stage to metamorphosis. a, anus; aa, anterior adductor muscle; af, apical flagellum; bg, byssus gland; bs, byssal spur used in laying down byssus threads; df, developing foot; f, foot; g, gut; l, digestive diverticulae; m, mouth; pa, posterior adductor muscle; s, stomach; st, statocyst; v, velum; vr, velum retractor muscles.

blooms, whereas larvae of some other bivalves remained apparently unaffected. In other situations larvae in the early stages of development were destroyed while the older larvae continued to live.

Studies of the type just outlined require, of course, the identification of the larvae in plankton samples; the present report is a contribution to the methodology of identification. In this report we give the sizes (length and width) of the 20 species of bivalve larvae reared at Milford Laboratory and the photomicrographs showing their shapes.

PROBLEMS IN THE IDENTIFICATION OF BIVALVE LARVAE

The difficulties in identification of larvae are due, in large measure, to a lack of knowledge of their shapes and dimensions from the time they attain the first shelled stage until they reach metamorphosis and change into juvenile mollusks (Fig. 1). Some authorities, as MacBride (1914), believed that the veliger larvae of bivalves are so similar in appearance and size that they cannot be distinguished at all and that the differentiation of various species takes place only during their post-larval life. Regardless of the difficulties mentioned by MacBride, several workers have given descriptions of the larvae of one or more species. The best known contributors to this field include Stafford (1912), Kändler (1926), Wells (1927), Lebour (1938), Miyazaki (1935, 1936), Werner (1939), Jørgensen (1946), Sullivan (1948), Rees (1950), Quayle (1952), Yoshida (1953, 1964), Imai and his co-workers, whose contributions will be mentioned later in this article, and Loosanoff & Davis (1950, 1963).

Some of these contributions have added considerably to our limited ability to recognize bivalve larvae. Others, however, were of questionable value because they were based, fully or partially, on specimens whose identity could not be established definitely. In other words, the authors used the "indirect method" of identification, assuming, often with no basis whatsoever, that a specimen was the larva of a certain bivalve. The "indirect method" also consisted, sometimes, of following the development of unknown larvae, taken in plankton samples, through various stages of growth to metamorphosis and occasionally past it. Even this procedure is not entirely dependable, however, because juvenile mollusks of many species are almost identical and, therefore, can be easily mistaken for each other.

Examples of errors from the "indirect method" are not uncommon in the literature on recognition and identification of bivalve larvae. For example, Stafford (1912) stated that the larvae of the common clam of the Atlantic coast, *Mercenaria* (=*Venus*) *mercenaria*, reached a size of approximately 450 microns (μ) before undergoing metamorphosis. In our experience of approximately 20 years of growing larvae of this species successfully, as well as in the experiences of our colleagues engaged in similar studies (Carriker, 1961), free-swimming larvae more than 240 μ long were exceptional. As a rule, most of the larvae of this clam metamorphose before they reach 220 μ. Consequently, the larvae described by Stafford exceed the maximum length of our larvae by over 200 μ. Since our larvae were grown from the eggs of known parents, under controlled conditions, the sizes of our larvae as compared to those of Stafford, clearly show that he was not describing the larvae of *M. mercenaria* but those of some other bivalve.

Several investigators have suggested that the size of lamellibranch larvae at the time of metamorphosis cannot be used as a criterion for their recognition because it may vary greatly with environmental factors, especially temperature. For example, Nelson (1921) suggested that the maximum size of the larvae of the American oyster, *Crassostrea virginica*, grown in Canadian waters should be larger than those grown in southern areas because of the lower water temperature in the north. If this were true, as Carriker (1951) pointed out, one would find smaller larvae in Delaware Bay, New Jersey, and even smaller individuals in the waters of the Gulf of Mexico. Later, Sullivan (1948) expressed the opinion that the larvae of the soft clam, *Mya arenaria*, in Canadian waters are considerably smaller at Malpeque Bay than at St. Andrews, where the temperature of the water is several degrees lower. Still more recently, Tanaka (1954) came to the conclusion that the larvae of the Japanese oyster, *Crassostrea gigas*, metamorphosed at different sizes in different localities. Tanaka's conclusions, however, were diametrically opposed to those of Nelson (1921) and Sullivan (1948) because he believed he had found that prodissoconchs of *C. gigas* of the northern waters of Japan were smaller than those of the southern areas. Consequently, according to Tanaka, the size at metamorphosis increased with increasing temperature.

We do not share the point of view expressed by any of the above-mentioned authors because in our extensive studies of the larvae of different bivalves, grown from known parents and under controlled conditions, we found no indication that such differences actually exist. Although we have grown larvae of *Crassostrea virginica* from parents brought from numerous points on the Atlantic and Gulf coasts, we have not discovered pronounced differences in their setting sizes. Normally, variations in maximum sizes of the larvae from the same area were greater than those between larvae from different areas. Our observations are supported by Carriker (1951) who, in studying the distribution of oyster larvae in New Jersey waters, found that the largest individuals in his samples were within the metamorphosing size range of our larvae originating from Long Island Sound parents.

In our work with another common species of the Atlantic coast, *Mercenaria mercenaria*, we again failed to detect significant differences in sizes of metamorphosing larvae whose parents came from widely separated sections of the Atlantic coast. Finally, in a series of experiments on rearing larvae of *M. mercenaria* at 5 different but constant temperatures, ranging from 18.0°-30.0°C, we found no significant differences with respect to their mean and maximum sizes at the time of setting (Loosanoff, 1959). Carriker's (1961) observations on the larvae of the same species in New Jersey waters proved that their sizes at metamorphosis agree closely with our findings on larvae of Long Island Sound and Massachusetts clams.

Furthermore, Stickney's (personal communication) work at Boothbay Harbor, Maine, with larvae of *Mya arenaria*, the parents of which were collected from Maine to Maryland, indicated that the median size of the metamorphosing larvae was between 200 and 235 μ, about the same as we observed for larvae of the same species native to Long Island Sound. Stickney stated further that he never saw larvae of either Maine or Maryland clams that were smaller than 180 μ or larger than 250 μ at metamorphosis. Thus, his observations almost duplicate ours (Loosanoff & Davis, 1963).

The inadequacy of the "indirect method" is well illustrated again by Rees (1950), who stated that: "For example, the larva of *Mytilus edulis* has been described about 10 times. Yet Jørgensen (1946) undoubtedly described a mixture of *Mytilus edulis* and *Modiolus modiolus* under the former species, and Lebour (1938) identified larvae as '*Mytilus* or relative'." According to Rees (1950) "The apparent uncertainty in the identification of *Mytilus* larvae is due to ignorance of the extent of inter-specific differences; are the larvae of *Modiolus barbatus*, for example, so like those of *Mytilus edulis*, that there is uncertainty in the identification of *Mytilus edulis*?". Rees stated openly that: "The surest method of determining the species of larvae is by culturing."

Rees also admitted that he was not certain all the larvae he described were truly pelagic and that, since most of the larval forms discussed in his paper had been identified by indirect means, some identification might have been in error. As we will show, Rees was correct in anticipating these errors. We think that the uncertainty expressed by Rees would have disappeared if the larvae of different species had been grown under laboratory conditions. Had Jørgensen (1946) as well as Rees (1950) had available photomicrographs and measurements of the larvae of *Mytilus edulis* and *Modiolus modiolus*, which are offered in this article (Figs. 7, 10), those authors would not have expressed uncertainty about the similarity of larvae of the 2 forms.

It would be unfair to criticize earlier workers for using the "indirect method" because at the time of the studies the art of rearing bivalve larvae was only in its beginning and, as much of the new information in that field had not been published, few people were aware of the simplicity and efficiency of the "direct method" (Loosanoff & Davis, 1950; Loosanoff, 1954). Clearly enough, Sullivan (1948) selected the "indirect method" because: "Special apparatus must also be provided and special techniques developed for rearing larvae since there are no standard methods available."

A comparison of several morphological characters of bivalve larvae, after they become shelled veligers, should aid in their identification. Most students agree that these characters are principally those of the shell rather than of the soft parts. Dimensions of the larval shell (prodissoconch), its general shape, prominence of the umbones during the progressive stages of growth from early straight-hinge stage to metamorphosis, and ratios of length of hinge to maximum shell length or width have been recommended as means of identification. Position of the larval shell ligament and, especially, the details of the hinge structure, including its teeth, also have been suggested as aids in identification by several authors, of whom Werner (1939) and Rees (1950) may be mentioned.

In our studies of larvae of 20 species of bivalves, all grown to metamorphosis under laboratory conditions from eggs of known parents, we attempted to evaluate features of their soft parts and, especially, their shells. We were interested also, after the appearance of Rees' paper, in developing a comparatively simple but rapid method of identification by hinge characters. In the course of this work we attempted frequently to photograph hinge structures of larval shells but, unfortunately, often found it difficult to obtain clear-cut pictures that could be used as easy guides to identification (Fig. 2).

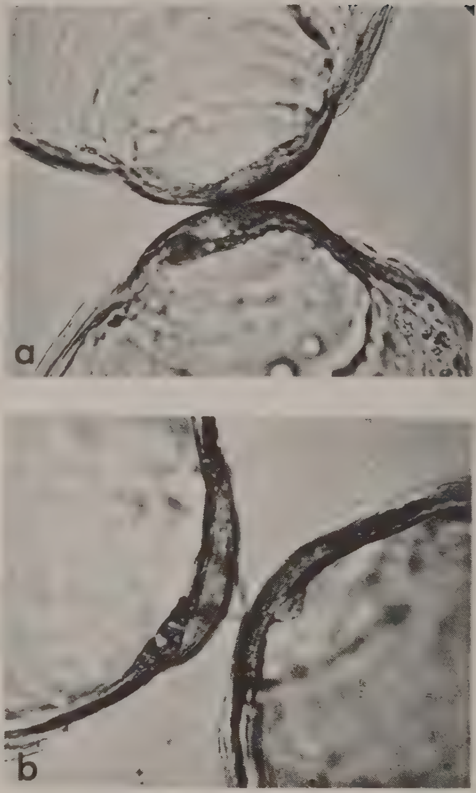


FIG. 2. Highly magnified photographs of internal surfaces of both valves of advanced veligers of (a) *Mercenaria mercenaria* (above) and (b) *Mytilus edulis* (below).

Moreover, from a practical point of view, considerable difficulties are involved in the use of hinge characters as a regular means of identification of larvae in plankton samples. Only freshly collected material can be used because, even if the larvae are preserved in a neutral formalin, the entire hinge structure may be altered by the preservative. Again, as our studies of some species have shown, the structure and general outline of the hinge changes with changes in size and shape of the larval shell. These observations indicate that to demonstrate the changes of the hinge structure of a larva of each species during the entire period of development, from straight-hinge to metamorphosis, an extensive series of photomicrographs of the hinge region would be required.

We also have found that if a relatively large number of larvae must be identified, it may be difficult to open and prepare them for microscopic examination within a reasonable time. A considerable dexterity is needed and, since the procedure is time-consuming, we doubt that this method will ever be used routinely by workers on plankton samples that contain the larvae of many species in different stages of development. If the procedure were relatively simple, we are certain that both Werner (1939) and Rees (1950), who so strongly recommended the use of the hinge apparatus as a means of identifying lamellibranch larvae, would have included photomicrographs of the hinges in their articles. Instead, both authors offered only schematic drawings of these structures. Moreover, although photographs of the hinge structure of larval bivalves have been published in several articles, Quayle (1952), working with *Venerupis pullastra*, is one of very few authors to give a good photomicrograph of the hinge area of the larval shell.

The existence of special structures, including teeth, in the hinges of larval bivalves is, nevertheless, undeniable. In many species these structures may be seen while the larvae are still in the straight-hinge stage. We are certain that, because of the considerable progress made during the last decade in culturing lamellibranch larvae in this country and Japan, the hinge structures of larval shells will soon be more comprehensively described, and good, readable photomicrographs of them obtained; as yet, however, they are not available. Finally, the lack of hinge structure in some species and the similarity between structures of others, make it possible that differences sufficient for the identification of closely related species may not be found.

A visual record of the outline of a larva during the period of its growth from straight-hinge stage until metamorphosis surely is one of the logical means of identification. Many bivalve larvae of the pelagic type, however, possess basically the same anatomical features and, because some of these features are not easily distinguishable in the early straight-hinge stages, this period is one when recognition of larvae presents a difficult problem.

The differences in shapes of molluscan larvae, nevertheless, are and will remain a criterion for identifying individuals of widely separated species. For instance, the general outlines of *Ostrea edulis*, *Crassostrea gigas* and *Mya arenaria* are so different that they are readily distinguishable (Figs. 19, 28, 55). Closely related forms, on the other hand, are hard to separate. For example, in some water basins we may find 2 or more species of the same genus whose larvae at all stages of development resemble each other so closely that it is virtually impossible to tell them apart. An example of this similarity is offered by 2 species of the genus *Crassostrea: C. virginica*, the eastern oyster (Fig. 25), and *C. gigas*, the oyster from Japan (Fig. 28), which have been introduced in several areas of our Pacific coast. Both species are found at present in Tomales Bay, California, although low water temperature prevents them from propagating every year. Nevertheless, spawnings occur occasionally and, when they do, the similarity of the larvae can make it virutally impossible to tell to which species they belong.

Similar problems may be encountered in waters where 2 species of the genus *Ostrea* are found. This situation is a definite possibility because we have introduced the European oyster, *O. edulis* (Fig. 19), in several areas of the Pacific coast (Loosanoff, 1951, 1955), where another species, *O. lurida* (Fig. 22), is native. Our recent observations on *O. edulis*, which were reared as spat at the Biological Laboratory in Milford, Connecticut, and then planted in Tomales Bay and Drake's Bay, California, have shown that these oysters bear the larvae in their gills as early as April. The dates of the end of spawning and swarming have not been determined but, on the basis of observations at Milford and the examination of a few oysters in California waters, we may assume that some of the larvae will be discharged as late as the beginning of October. Larvae of *O. lurida* will probably be found in the same waters during the same time. Thus, during a period of several months, extending approximately from April until October, the larvae of the 2 species will be present in the same environment and, because of their similarity, will be extremely difficult to tell apart.

The recently developed technique of growing bivalve larvae from fertilized eggs to metamorphosis under controlled conditions has also provided us with a second aid for their identification: the dimensions of the larvae during different stages of their growth. The measurements reported in this paper are expressed in microns and refer to the length and width of the larval shells. The length measurement represents the longest distance along the anterior-posterior line of the shell, roughly parallel to the hinge. The width is the distance from the tip of the umbo to the ventral margin of the shell. Some authors prefer to call the latter measurement "depth" or "height". However, we will continue to call it "width" for several considerations, the principal being that numerous publications by members of the Milford Laboratory employ the words "length" and "width" to describe larval sizes (see Loosanoff & Davis, 1963). A change of our commonly used term "width" to a less familiar "depth" or "height" could create confusion. Moreover, measurements of post-larval and adult forms of many bivalves, such as *Mercenaria mercenaria* and other clams, are expressed in terms of "width" rather than "depth" or "height". Our terminology therefore seems to be most logical in the study of the entire life histories.

Workers who attempt to identify the larvae of different species may find the length-width data which we offer of value because they give, for each species, the possible range in width for the larvae of each length. Furthermore, our data indicate the frequency with which each width occurs at a given length. For example, the widths recorded for the larvae of *Arca transversa*, which measured 130 μ in length, ranged from 100-115 μ (Fig. 5). Of the 60 larvae of that length, however, only 12 individuals were 100 μ wide, 39 were 105 μ wide, 8 were 110 μ wide, and only 1 was as wide as 115 μ. Thus, a worker who encounters a larva 130 μ long and suspects that it is *A. transversa* can, by noting its width, refer immediately to our length-width curve to estimate the probability that the larva belongs to that species.

Larvae of some bivalves, such as *Ostrea edulis* and *O. lurida*, may, in the last stages of growth, measure as much as 200 μ in thickness if the measurement is taken near the hinge. Under the microscope, therefore, the larvae may appear as thick wedges tapering rapidly from the hinge to the sharp ventral side. This circumstance makes it difficult to obtain accurate measurements of the larval thickness and may also explain the considerable variations in the width measurements of larvae with the same length. For example, widths of larvae of *O. edulis* 230 μ long may vary from 185-220 μ, *i.e.* about 35 μ (Fig. 23). Conversely, the relative roundness of the larvae may influence the accuracy of the length measurements because the larvae 210 μ in width may vary from about 225-265 μ in length. The same difficulties are encountered in measuring the larvae of other species with thick umbones. These facts must be taken into consideration in forming conclusions based on shell measurements.

From the measurements now available it is also possible to offer length-width relationships of larvae of different sizes and to calculate the formula for the regression of width on length for each species. For example, the length-width data of *Crassostrea gigas* give a regression equation of $W=1.104\ L-8.94$, while the same value for *Ostrea lurida* is $W=0.897\ L-4.1$. The difference between the regression lines of these 2 genera is statistically significant. On the other hand, the median lines fitted by visual examination for the length-width data on our graphs make it evident that regression lines for the larvae of *C. gigas* and *C. virginica* are so similar that they probably cannot be distinguished mathematically. The same is true of the larvae of *O. edulis* and *O. lurida*. We are continuing the mathematical analysis of the data and shall present the results of these studies in a separate article. Although these results may be of considerable theoretical interest, they probably would not help significantly in routine identification of the larvae in plankton samples.

The length and width measurements, although helpful in distinguishing the larvae of different genera, may be of little value in identifying larvae of closely related forms, such as *Crassostrea virginica* and *C. gigas* or the two species of the genus *Ostrea*, because measurements of the larvae of the 2 related species are almost identical.

The color of larvae has been suggested by some authors as one of the characters on which their identification could be based (Sullivan, 1948). We do not agree that it is a dependable criterion because we have noticed frequently that the color of laboratory-grown larvae, especially in the early stages of development, depends to a large extent on the color of the food they consume (Loosanoff & Davis, 1950). Since the color may be changed under laboratory conditions by feeding the larvae different foods, it may be assumed that in nature, where the quality and quantity of plankton, especially phytoplankton, undergo almost continuous change, the color of the larvae may be correspondingly affected. This view applies principally to younger stages, whereas the color of the older larvae with well-developed, heavy, thick shells may not be easily altered. The changes in color are due, of course, to the changes in color of the digestive tract.

Quayle (1952) was also of the opinion that the loss of color of veligers upon preservation makes color differences, even if sometimes displayed by living larvae, valueless to students of plankton. Certain other anatomical details, such as eye spots or the position of the digestive gland, likewise become fainter or disappear entirely soon after preservation. It is principally the outline of a prodissoconch, including degree of slope from umbone anteriorly and posteriorly, its size, and the hinge teeth when present, that will help most in identifying a larva. However, the hinge structure may also soon become useless by being partly dissolved by the preserving fluid if specimens are kept in formalin that is only slightly acid.

In this article we offer a series of photomicrographs of larvae of 20 species of bivalves in different stages of their growth and development. All the larvae were grown under contolled conditions from the eggs of known parents or released by them in swarming. Our photomicrographs show a succession of sizes and shapes of the larvae of each species, from early straight-hinge stage to the maximal or nearly maximal size.

Whole specimens were used for photography, although we realize that only the use of a single valve makes it possible to avoid the tilt of the umbo region, a condition which may change considerably the outline of a larval shell. Because most workers will deal with the entire animal, not with a single valve, they will see the larvae in positions similar to those given in our photographs. We prefer, therefore, to show photomicrographs of whole larvae with the 2 valves intact. We hope that the material offered will help workers engaged in studies of zooplankton in general and bivalve larvae in particular.

Since bivalve larvae have been described frequently, it would be superfluous to repeat the detailed descriptions. We offer, therefore, only a diagrammatic drawing showing the major features of a typical bivalve larva during several stages of its development (Fig. 1). Those interested in more detailed descriptions of larval structure should refer to the articles on their morphology offered by several authors, the most recent by Quayle (1952) and Ansell

(1962). The list of references in Ansell's paper should be helpful in pursuing the studies further.

We admit that we still do not have a fully dependable, simple method to identify easily the larvae of most species of bivalves. We have, nevertheless, several reliable means that, under certain conditions, may be extremely helpful. We offer especially the series of photomicrographs of the larvae showing their shapes and also give extensive data on their length and width. Use of these 2 criteria may resolve readily many problems of identification which appeared insoluble only a decade or so ago.

We believe also that, since the methods for culturing bivalve larvae are continuously being improved, better means for studies of their differences, applicable in field work, may become available. Chemical methods for the identification of larvae eventually may be used. Some of them may be based on differences in the enzyme complement of different species. In this method, a change of color when the larvae are placed in solutions of certain chemicals may indicate to which family, or perhaps even genus, they belong. It is also possible that microserological and micro-chromatographic methods can be applied.

The material for this article was collected over a period of approximately 15 years. At first we did not contemplate preparation of a paper describing the larvae of different species, and it was considerably later, only after we realized how much valuable material had accumulated, that we decided to summarize it in the present form. At the beginning of these studies our techniques were less refined than they are now. As a result, the quality of photographs of the larvae of different species varies. Those of the earlier period are somewhat inferior to those taken later. Several members of our staff took the pictures of the larvae used in this article, and during this long period different cameras, microscopes, and sources of illumination had to be used. Because of these circumstances the photographs of some species may appear lighter than others. The density of the photographs should not be considered a criterion for identification. For the same reasons the magnifications of the photomicrographs of all species of the larvae are not identical. Rather than give magnifications of the larvae, we offer the actual dimensions in microns.

Finally, some photographs, especially of the early larval stages, may have dark backgrounds. This defect is almost unavoidable because the young larvae are sometimes so transparent that to obtain sharp outlines the background of the photograph must appear dark. We hope, nevertheless, that these imperfections will be overlooked because a repetition of the studies needed to prepare more uniform photographs would require many years of persistent work.

Miner (1950) and Abbott (1954) provided most of the information on the geographical distribution of the different species. Sequence of the species in the manuscript is given also largely according to Abbott. The notable exception is *Laevicardium mortoni*, at the end of the list. This placement is not for reasons of classification but because we do not have a series of 4 photomicrographs of the groups of larvae of *Laevicardium* similar to those of the other 19 bivalves described in this article.

PREPARATION OF PERMANENT MOUNTS OF WHOLE LARVAE

Soon after we began rearing bivalve larvae it was decided to preserve them as whole mounts to provide a permanent record of their size and general outline. We thought that preparations of this type would be useful to students working on recognition of bivalve larvae in plankton collections and also for other studies of these organisms. After trying a variety of methods of preparing the slides we adopted the following technique, which gives satisfactory results, especially if the last 2 steps of passing the specimen through a mixture of alcohol and xylene are closely followed:

1. Kill and fix in 3.0% neutral formalin, using 40% commercial formalin as 100%, 30 minutes to 1 hour
2. Alcohol: 35%, 5 minutes
3. Alcohol: 50%, 5 minutes
4. Alcohol: 70%, 5 minutes
5. Alcohol: 80%, 15 minutes
6. Alcohol: 95%, 30 minutes
7. Alcohol: 100%, 15 minutes
8. Alcohol: 100%, 10 minutes
9. 3 parts of 100% alcohol + 1 part of xylene, 5 minutes
10. Equal parts of 100 % alcohol and xylene, 5 minutes
11. One part of 100% alcohol + 3 parts xylene, 5 minutes
12. Xylene, 5 minutes
13. Mount from xylene in synthetic resin mounting medium and place the cover glass on it.

It is sometimes advantageous to color the larvae artificially to bring out more clearly their outlines and internal structures in the final preparation. The living larvae are placed in a solution of 1 mg of Neutral Red in 1 liter of sea water for about 1-1/2 hours before killing and fixing them (Loosanoff & Davis, 1947). After the larvae acquire sufficiently dense color they are collected on a fine screen, washed and processed. If the Neurtral Red stored by the larvae in their bodies before fixation is partly lost during processing, it may be desirable to add to all alcohol solutions a few drops of Brilliant Vital Red (Evans) to restore the color.

During processing larval samples are carried from one solution to another in a small container made of the upper part of a small vial with a piece of number 20 silk bolting cloth or correspondingly fine plastic mesh securely tied around the lip. The fluid passes through the cloth, but the larvae are retained. This device, which one of us has used for more than 35 years, simplifies greatly the problem of preparing whole mounts of small organisms, including phytoplankton.

Slides prepared in this way have been distributed to students of bivalve larvae in several countries. Many sets of slides are still in use and in good condition. We believe that these slides, in combination with the series of photomicrographs and length-width measurements of the larvae which we offer in this article, will help significantly in identifying larvae.

DESCRIPTION OF DIFFERENT SPECIES

1. *Arca transversa* Say

This species, known by the common names Transverse Ark Shell or Blood Clam, ranges from New England to the Florida Keys, and in some areas, including Long Island Sound, is comparatively numerous. It is a member of the Family Arcidae, several representatives of which are found within the same range of distribution as *Arca transversa*.

The larvae of this species resemble, in general, the rhomboidal shape of the adults; the umbo is directed slightly forward. The resemblance between the shapes of the larvae and the adults becomes especially noticeable as the former approach metamorphosis (Figs. 3, 4).

The smallest normal straight-hinge larva in our cultures was 70 μ long and 55 μ wide. The early straight-hinge larvae are usually somewhat larger, however, approximately 75 x 57 μ (Fig. 5). The difference between length and width of the larvae is large. Among the youngest straight-hinge individuals it may be approximately 20 μ, and at the time of metamorphosis the length may exceed the width by almost 70 μ (Fig. 5). Widths of larvae of the same length also vary considerably. For example, among 24 larvae all 255 μ long, widths ranged from 175-200 μ.

Larvae of the early straight-hinge stage are considerably darker than the larvae of corresponding stages of most

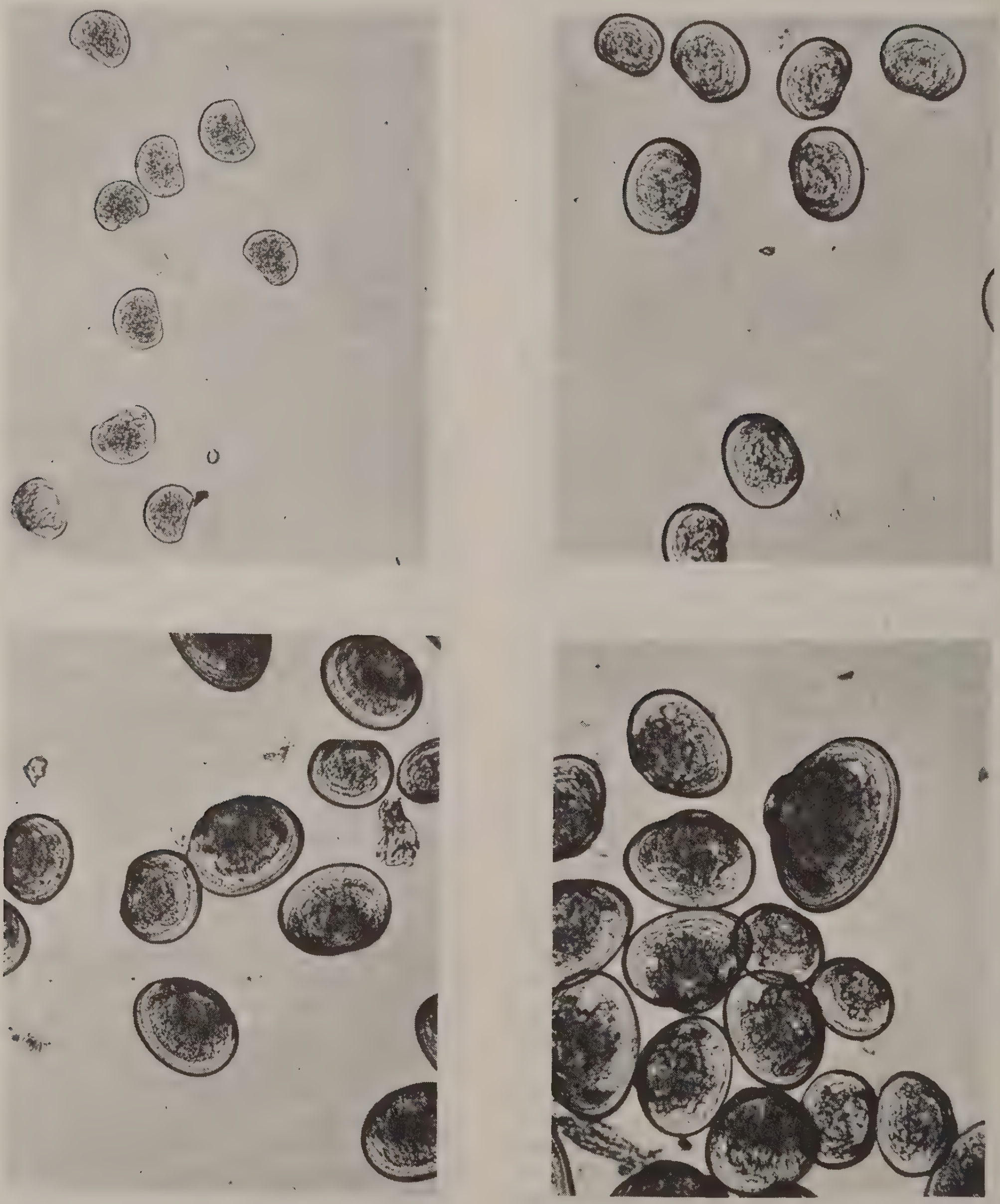


FIG. 3. Group photographs of different sizes of larvae of *Arca transversa*. Smallest individuals of the youngest group are approximately 70 μ long, and the largest of the oldest, approximately 230 μ.

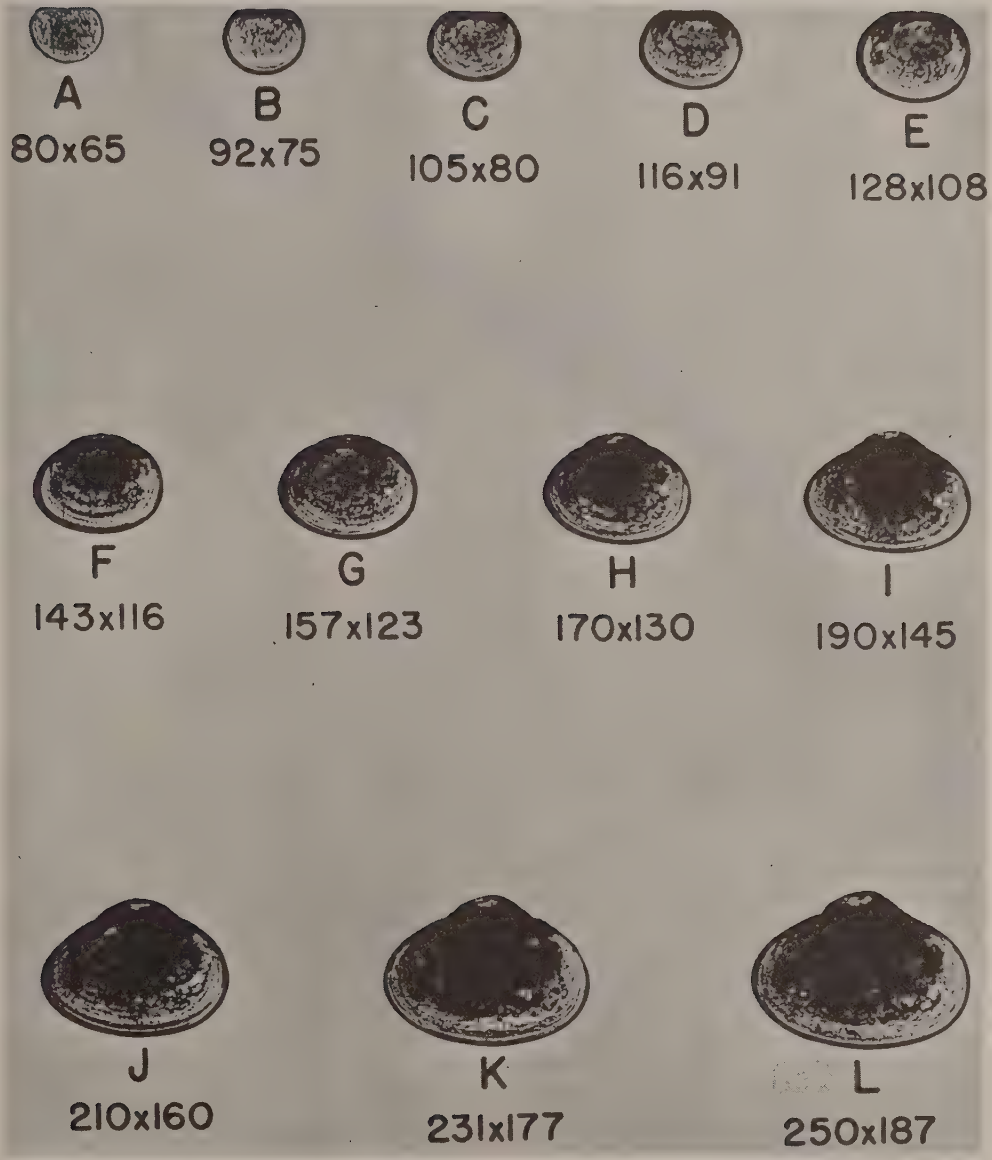

A
80x65
B
92x75
C
105x80
D
116x91
E
128x108
F
143x116
G
157x123
H
170x130
I
190x145
J
210x160
K
231x177
L
250x187

FIG. 4. Photographs of larvae of *Arca transversa* in different stages of development from early straight-hinge stage (A) to the stage of metamorphosis (L). Measurements are in microns; the first figure under a photograph indicates length, and the second, width of the larva.

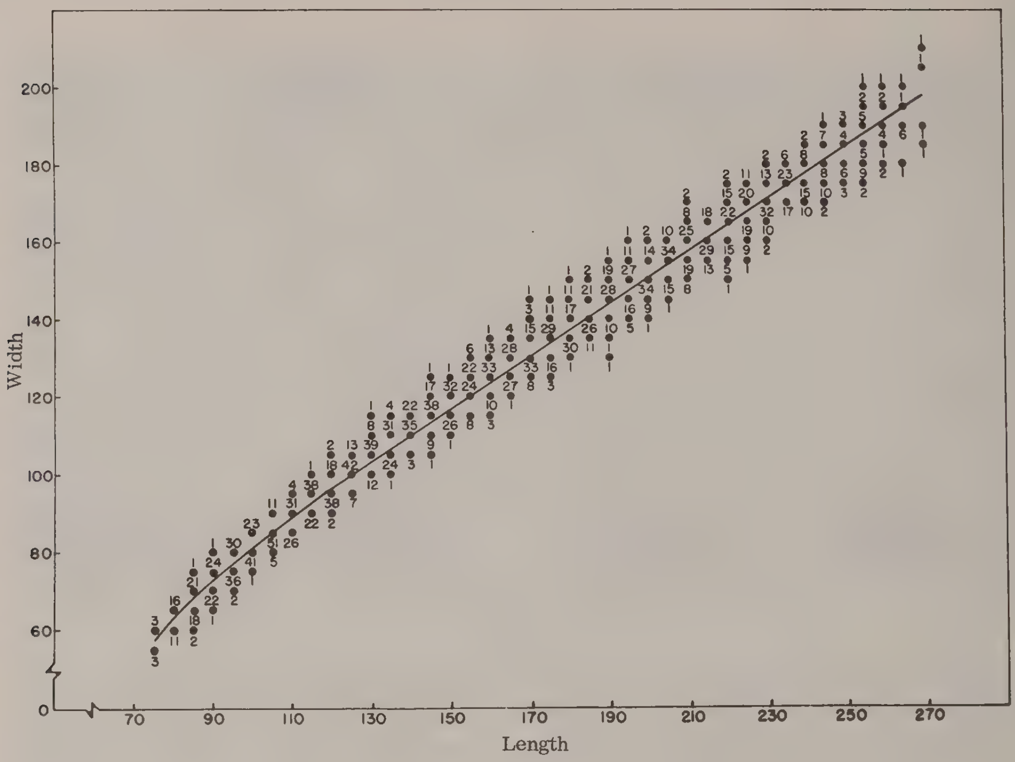


FIG. 5. Length-width relations of larvae of *Arca transversa* during the entire free-swimming veliger stage. Measurements in microns. The figures at dots indicate the numbers of larvae of each dimension.

other species, and they become darker as their size increases. In living, laboratory-reared larvae, the pointed end of the shell normally displays a reddish-brown color when the individuals reach approximately 140 μ in length, while the opposite, or more rounded end remains brown. An "eye" spot usually appears at the length of about 225 μ and becomes more conspicuous as the larvae approach metamorphosis. In some individuals, however, especially those growing at a comparatively slow rate, the "eye" spot may be seen in larvae only about 205 μ long. An umbo begins to form when the larvae reach about 110 μ in length and is normally well-defined at the length of 130 μ (Fig. 4).

The majority of normal larvae begin to metamorphose at lengths ranging between 240 and 260 μ. However, as already reported for bivalve larvae in general (Loosanoff *et al.*, 1951; Loosanoff & Davis, 1963), considerable variations in setting sizes of *Arca transversa* are normal. For example, some larvae were only 215 μ long at metamorphosis, whereas others, possibly abnormal in some respects, were considerably larger than 260 μ. One individual of 310 μ was seen still swimming although it had already developed a large foot. Possibly it had already metamorphosed. Some individuals in the later stages of metamorphosis already possess a byssus with which they can attach themselves to suitable surfaces.

The literature on *Arca transversa* contains no references describing its spawning or larval development. It appears certain, however, that this clam spawns during late spring because some individuals brought from Long Island Sound to the laboratory in the middle of May spawned within 2 or 3 hours after being placed in warm water (Loosanoff & Davis, 1963).

2. *Mytilus edulis* Linnaeus

The mussel family includes some of the most common and abundant species of bivalves. *Mytilus edulis* is probably one of the best-known representatives of the group. On our Atlantic coast it is found from the Arctic to North Carolina, and on the Pacific coast, from Alaska to California. These mussels are also numerous along the European shores, where they support important fisheries.

Because of their common occurrence, the larvae of *Mytilus edulis* have been described by a number of authors, including Borisjak (1909), Werner (1939), Jørgensen (1946), Sullivan (1948), Rees (1950) and Loosanoff & Davis (1963). The smallest straight-hinge larvae of the mussels grown in our cultures were approximately 94 x 64 μ, and the largest measured about 300 x 286 μ (Figs. 6, 7, 8).

Live mussel larvae display an "eye" spot, from 5-7 μ in diameter, near the center of their bodies. This spot appears when the larvae are approximately 215 μ long. Normally, all larvae about 230 μ or longer possess the "eye" spot. A well-developed foot may appear in larvae as small as 185 μ long, although normally the first signs of the foot are noticed when the larvae approach 210 μ. At the length of about 235 μ the majority of the larvae already possess this organ.

The smallest metamorphosed individual, found already attached by its byssus to old oyster shell placed on the bottom of our culture vessels, measured only about 215 x 200 μ. Fully metamorphosed mussels, also attached by a byssus but only 225 μ long, were not uncommon. In some cultures, however, larvae almost 300 μ in length were still swimming actively. Thus, the length at which mussel larvae metamorphosed in our cultures varied by nearly 90 μ.

Stafford (1912) reported that the largest swimming larvae of the mussel were 400 x 330 μ. It is doubtful that he actually measured the larvae of *Mytilus edulis* because his measurements are so different from ours made on larvae of known origin. Nelson (1928) also reported that the size of the larvae was much larger than ours. According to him the largest swimming larvae of *M. edulis* measured 376 x 344 μ. He stated that recognition of the larvae of this species is made easy because of their small width. Although this is true of most straight-hinge stages, the larger larvae become relatively wider (see Figs. 7, 8). Furthermore, Nelson's measurements contradict his contention as to the relatively small width of his larvae. Finally, photomicrographs of the larvae given by Nelson show at least one individual in which the length and width are almost identical.

Werner's (1939) measurements of length and width of the larvae of *Mytilus edulis* agree, in general, with ours, except that he gave the measurement of his smallest larvae as approximately 112 x 84 μ, which is considerably larger than the dimensions of our smallest larvae (Figs. 7, 8). Jorgensen (1946) commented on the remarkable peculiarities of the larvae of *M. edulis* because of the extensive variability of their shape and color of the shell. He also mentioned the large differences in sizes of larvae undergoing metamorphosis.

Sullivan (1948) reported that the larvae of *Mytilus edulis* ranged from about 155 x 120 μ to about 355 x 320 μ. Sullivan's data indicate, therefore, that her measurements of the smallest larvae were approximately 60 μ larger than ours, whereas her largest larvae measured about 50 μ more than the lar-

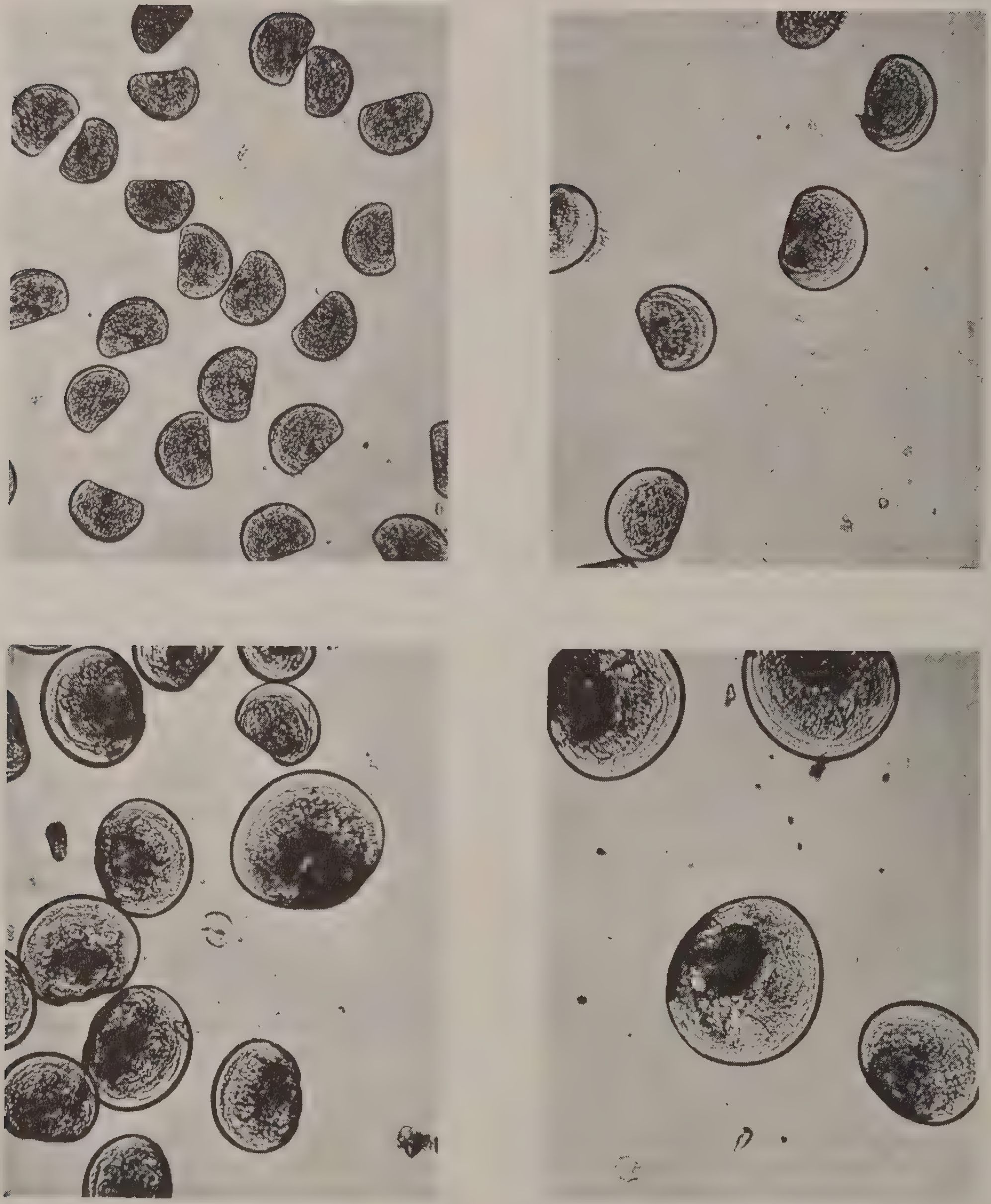


FIG. 6. Group photographs of different sizes of larvae of *Mytilus edulis*. Smallest individuals of the youngest group are approximately 90 μ long, and the largest of the oldest, approximately 225 μ.

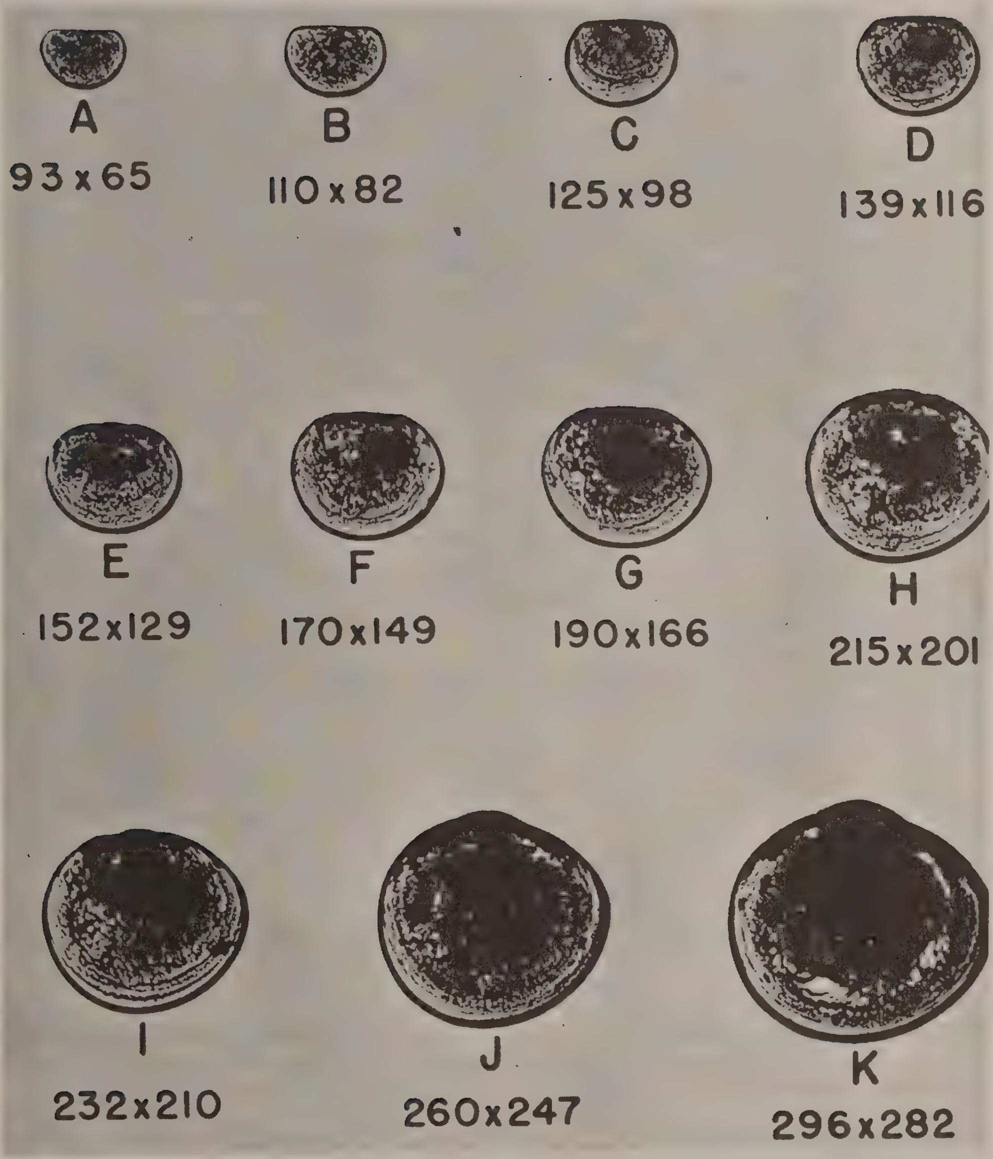

A
93x65
B
110x82
C
125x98
D
139x116
E
152x129
F
170x149
G
190x166
H
215x201
I
232x210
J
260x247
K
296x282

FIG. 7. Photographs of larvae of *Mytilus edulis* in different stages of development from early straight-hinge stage (A) to the stage of metamorphosis (K). Measurements are in microns; the first figure under a photograph indicates length, and the second, width of the larva.

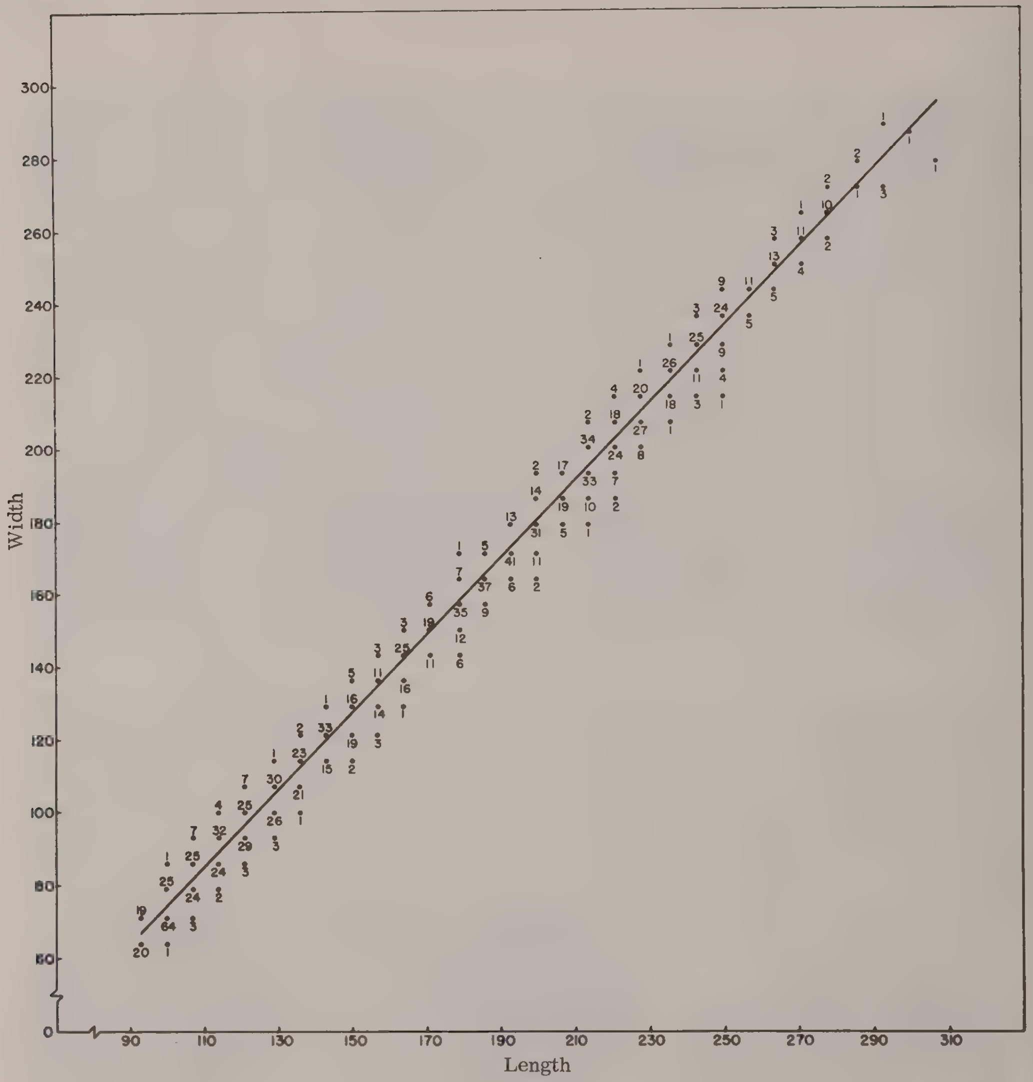


FIG. 8. Length-width relations of larvae of *Mytilus edulis* during the entire free-swimming veliger stage. Measurements in microns. The figures at dots indicate the numbers of larvae of each dimension.

gest larvae in our samples.

Rees (1950) stated that straight-hinge larvae of both *Mytilus* and *Modiolus* have similar shapes though in *Modiolus* the narrow end of the shell is less pointed than in *Mytilus*. In more advanced stages, however, the shape and general outline of the larvae of these 2 forms become increasingly different.

3. *Modiolus demissus* (Dillwyn)

Modiolus demissus, the common ribbed mussel of the Atlantic coast, is also called *Volsella demissus*, *V. plicatula*, *M. plicatula* and several other names. It ranges from Prince Edward Island to South Carolina and Georgia. In some areas it is extremely abundant, especially in tidal marshes, on mud flats and among the rocks a few feet above mean low-water mark.

At the early straight-hinge stage most of the larvae of *Modiolus demissus* measure from 110-115 μ in length and from 85-95 μ in width, although occasionally smaller individuals, only about 105 μ long, are found in cultures (Figs. 9, 10, 11). A few larvae develop a functional foot and a prominent "eye" spot at the length of about 200 μ, and some may metamorphose at only about 220 μ long. These larvae are exceptional, however, because the majority do not lose their vela until they are approximately 275 μ long. In some cultures a few individuals still possessing a functional velum were about 300 μ long. Thus, while we agree with Sullivan (1948) on the size of the smallest straight-hinge larvae of this species, our largest larvae, measuring approximately 305 x 260 μ, were considerably larger than the maximum size of 205 x 170 μ given by her.

Despite the common occurrence of *Modiolus demissus*, Sullivan's article was the only reference we found that described the larvae of this species. Partial descriptions of the larvae of *M. modiolus*, and other closely related forms, have been offered, however, by Werner (1939) and Jørgensen (1946). Jørgensen suggests a close resemblance between the veligers of *M. demissus* and *Mytilus edulis*. We find, however, that the larvae of these 2 presumably closely related species are different in their length-width ratios and also in their general appearance when they are near metamophosis (compare Figs. 7, 10). We may add also that the photomicrographs of the larvae of *Modiolus modiolus* given by Rees (1950) show that the shapes of larvae of this species appear to be rather different from those of larvae of *M. demissus* grown at our laboratory.

4. *Anomia simplex* D'Orbigny

This mollusk, commonly called the Silver or Jingle Shell, is abundant from Nova Scotia to the West Indies. It is extremely numerous during some summers in Long Island Sound where it sets, together with the new generation of oysters, on old shells and rocks, competing with the oyster set for space and food.

Larvae of *Anomia* have been described by a number of workers, including: Stafford (1912) and Sullivan (1948), who gave descriptions of *A. aculeata;* Miyazaki (1935), who described the larvae of the Japanese species, *A. lischkei;* Lebour (1938) and Jørgensen (1946), who offered descriptions of *A. squamula;* and Rees (1950), who referred briefly to 3 species of *Anomia*.

The smallest larvae in our cultures measured about 58 x 47 μ, although young straight-hinge larvae are normally somewhat larger (Figs. 12, 13, 14). During the early stages of development the length of the larvae is about 10 μ greater than the width. Later, when the length reaches approximately 135 μ, the width increases more rapidly than the length, and during the final stages the two dimensions are almost identical (Fig. 13).

Considerable difference is noticeable in the shape of the 2 shells of a larva even during the early straight-hinge stage. Normally, one shell is well rounded, while the other, which becomes the lower when the animal is attached, is nearly flat. This difference is noticeable at all stages of larval development. Moreover, the umbo of the right shell is not well developed. Jørgensen (1946) made the same observation on the shells of *Anomia squamula*.

During early development the shells of the larvae of *Anomia simplex* are almost transparent and nearly colorless. Even when the larvae approach metamorphosis their shells remain transparent. Because of the prominent umbo developed during advanced stages, the larvae of *A. simplex* may be mistaken for those of oysters of the genus *Crassostrea*, which also have a protruding umbo. This mistake can be avoided by remembering that

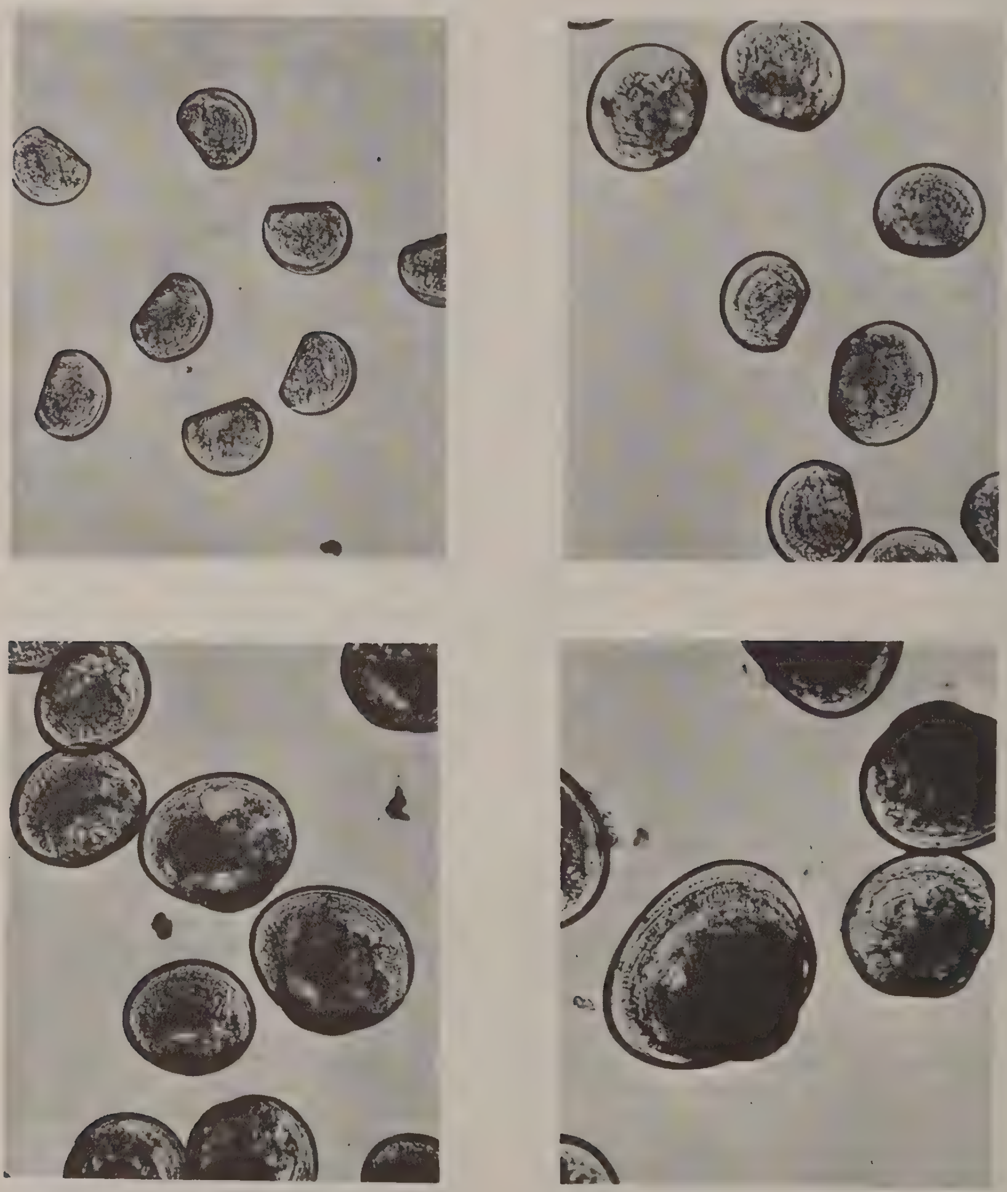


FIG. 9. Group photographs of different sizes of larvae of *Modiolus demissus*. Smallest individuals of the youngest group are approximately 105 μ long, and the largest of the oldest, approximately 290 μ.

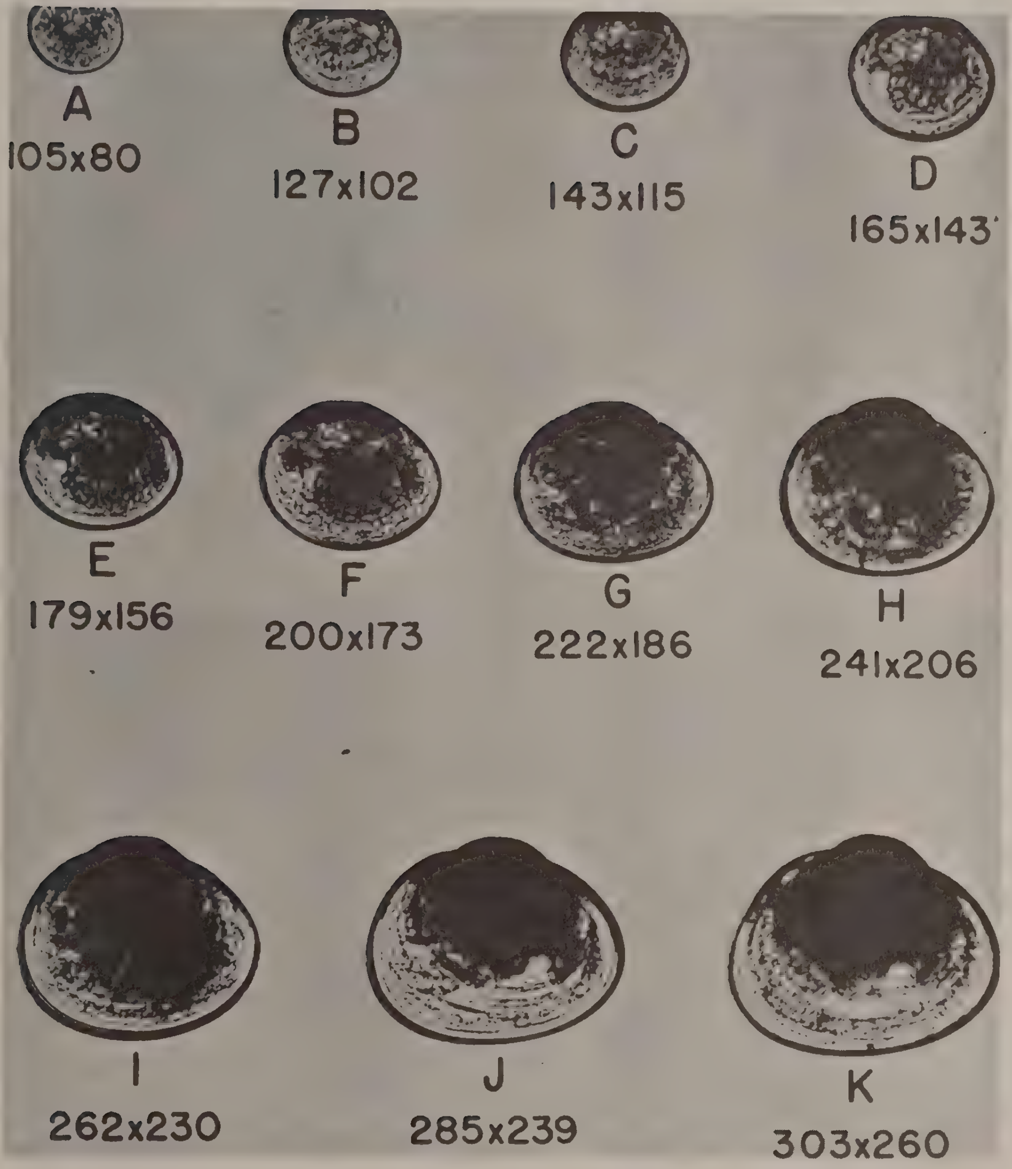

A
105x80
B
127x102
C
143x115
D
165x143
E
179x156
F
200x173
G
222x186
H
241x206
I
262x230
J
285x239
K
303x260

FIG. 10. Photographs of larvae of *Modiolus demissus* in different stages of development from early straight-hinge stage (A) to the stage of metamorphosis (K). Measurements are in microns; the first figure under a photograph indicates length, and the second, width of the larva.

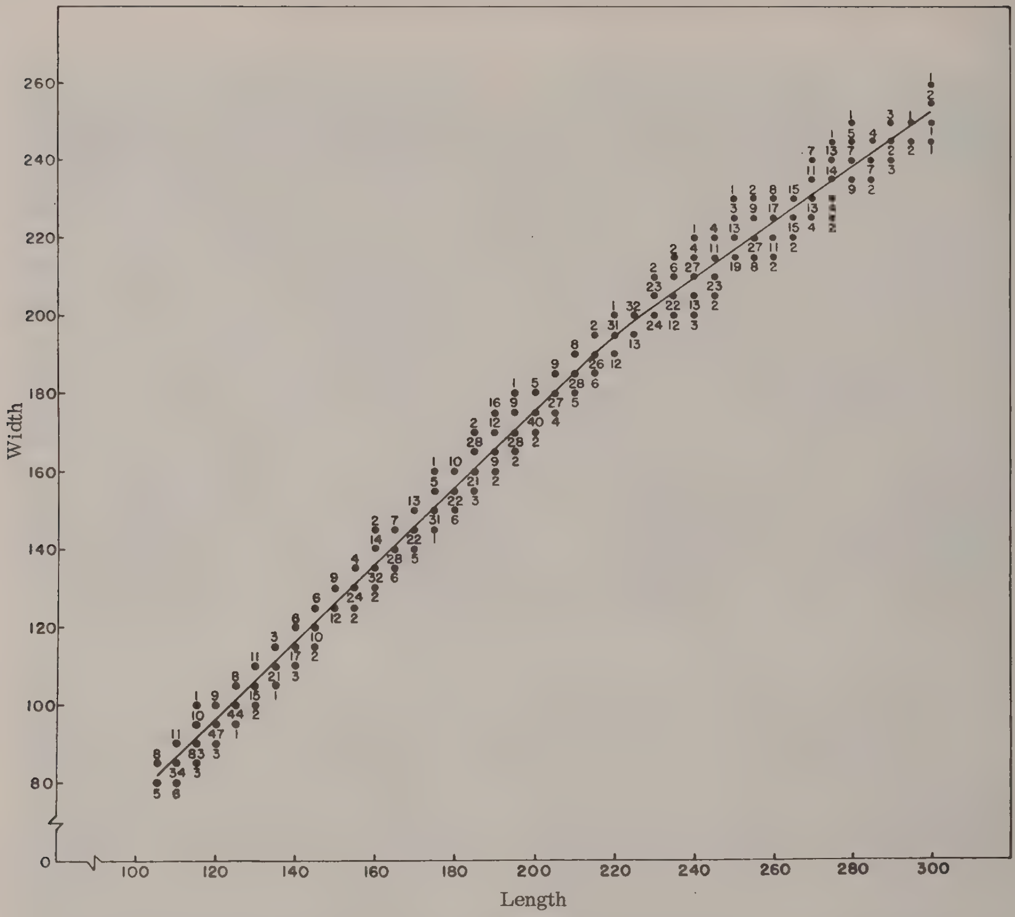


FIG. 11. Length-width relations of larvae of *Modiolus demissus* during the entire free-swimming veliger stage. Measurements in microns. The figures at dots indicate the numbers of larvae of each dimension.

in *A. simplex* the digestive organs are located almost beneath the umbones, or much higher than in the larvae of *C. virginica* or *C. gigas*. Moreover, the umbo of *Anomia* points straight up from the hinge line, whereas the umbo of *Crassostrea* slants posteriorly.

The indentation known as the byssus notch, which, according to some authors, is a diagnostic feature of *Anomia* larvae, could not always be found in our specimens. Sometimes, however, this notch was seen in larvae only about 180 μ long. Even then, it was often only a thickening of the shell edge on the side opposite the foot (Figs. 12, 13).

An "eye" spot could not be found in all larvae, even those that were approaching metamorphosis. In other individuals, however, the "eye" was observed when they were relatively small, only about 135 μ long. Usually the "eye", composed of 4-6 united dark bodies, appeared in the larvae when they were approximately 160 μ long.

Metamorphosis of larvae of *Anomia*

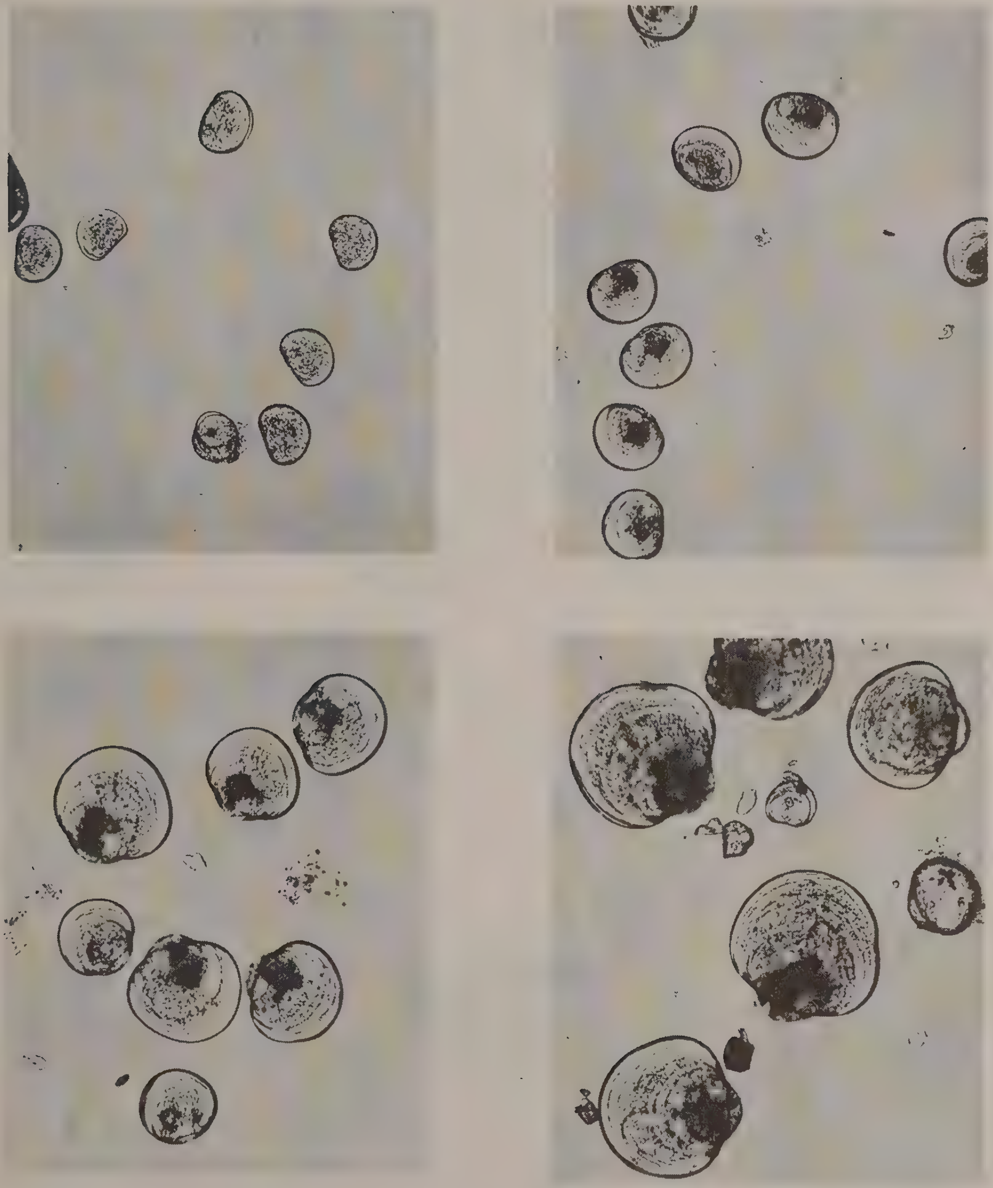


FIG. 12. Group photographs of different sizes of larvae of *Anomia simplex*. Smallest individuals of the youngest group are approximately 65 μ long, and the largest of the oldest, approximately 205 μ.

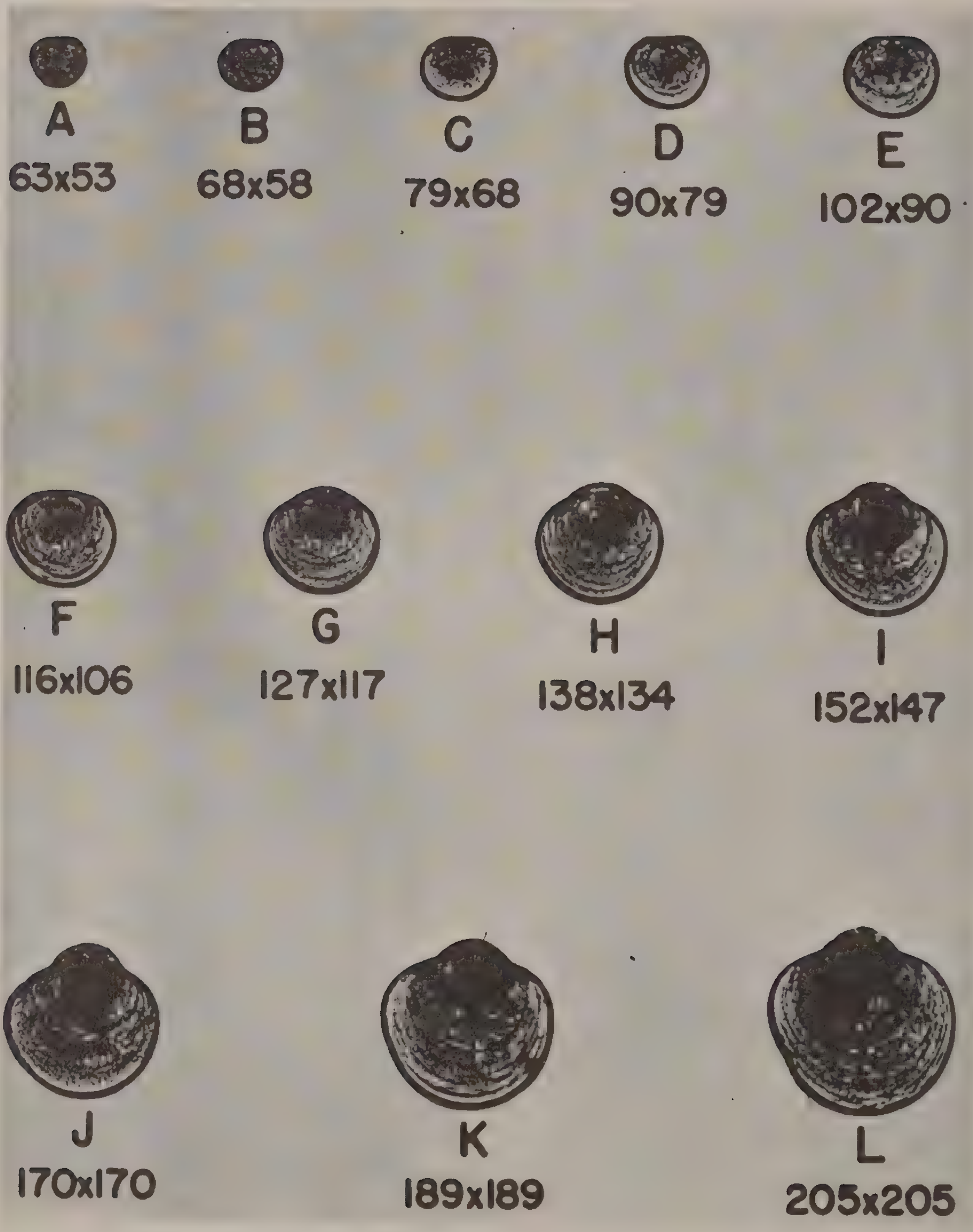

A
63x53
B
68x58
C
79x68
D
90x79
E
102x90
F
116x106
G
127x117
H
138x134
I
152x147
J
170x170
K
189x189
L
205x205

FIG. 13. Photographs of larvae of *Anomia simplex* in different stages of development from early straight-hinge stage (A) to the stage of metamorphosis (L). Measurements are in microns; the first figure under a photograph indicates length, and the second, width of the larva.

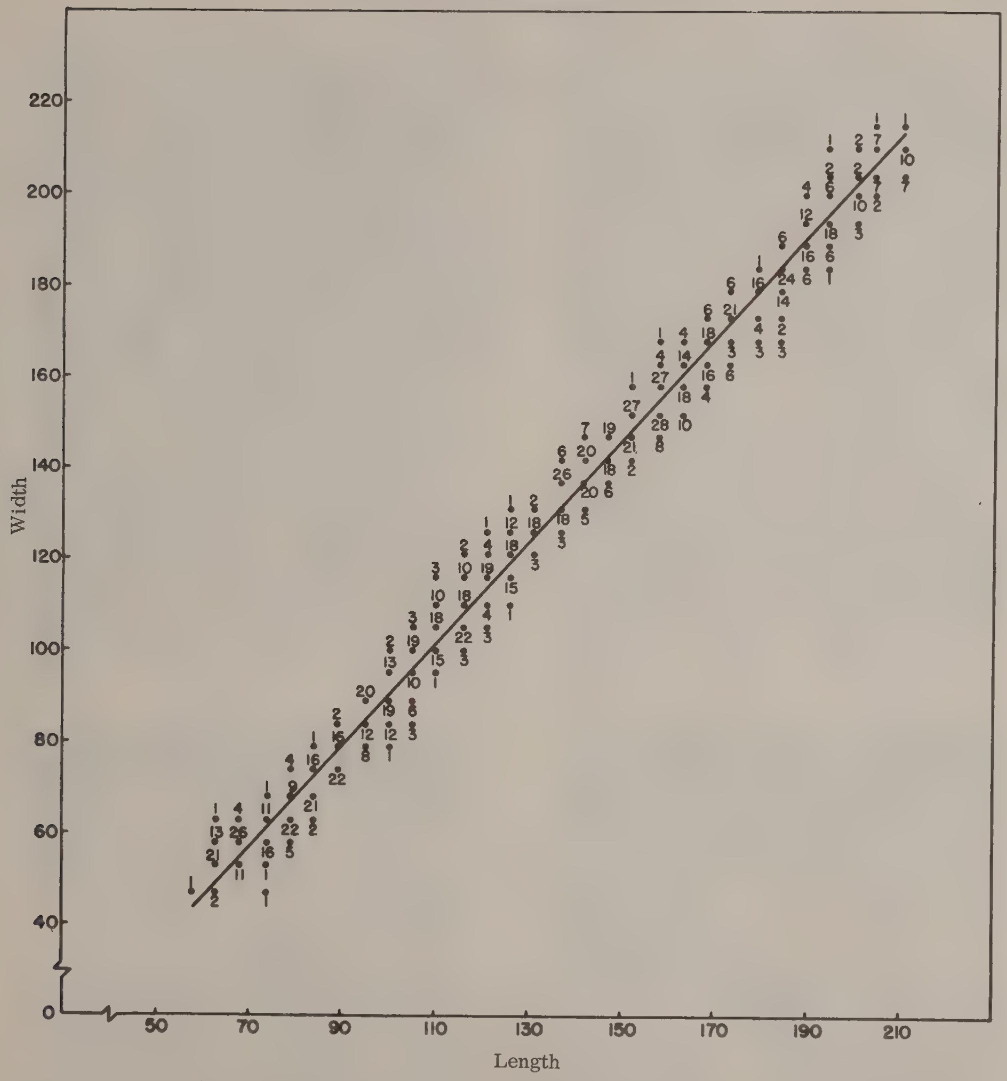


FIG. 14. Length-width relations of larvae of *Anomia simplex* during the entire free-swimming veliger stage. Measurements in microns. The figures at dots indicate the numbers of larvae of each dimension.

simplex sometimes begins when the individuals are only slightly more than 180 μ long. Most metamorphosing larvae, however, measured between 195 and 210 μ; the largest swimming larvae were approximately 215 μ x 220 μ (Loosanoff & Davis, 1963).

Many larvae of *Anomia simplex* grown under laboratory conditions displayed an extremely interesting phenomenon called "partial metamorphosis" (Loosanoff, 1961). This condition is characterized by the disappearance of the velum but retention of a functional foot past the size at which metamorphosis and attachment normally occur. Even though some of these individuals measured approximately 500 μ, they were apparently unable to attach to the substratum. These individuals had one pecularity in common, namely, the presence of a definite, narrow band on their shells. This band probably indicated the edge of the prodissoconch, or larval shell, and the beginning of the dissoconch, or post-larval shell. A similar abnormality may perhaps be observed in larvae of other species of the genus *Anomia* living under natural conditions, when some factors in their environment are unfavorable for metamorphosis.

5. *Aequipecten irradians* (Lamarck)

Aequipecten irradians, the common scallop of our Atlantic coast, sometimes identified as *Pecten irradians*, extends from Nova Scotia to the northern half of Florida and is also found along the coast of Texas. According to Clarke (1965) there are 3 distinct subspecies of this scallop; the type with which we worked, *A. i. irradians*, is found from Massachusetts to New Jersey.

Embryonic development of the scallop has been described by several students, including Costello *et al.* (1957), who offered a good review of the literature on this aspect of the scallop's life history. The more advanced stages, however, straight-hinge and later, have never been described in detail. Wells (1927), who grew the larvae of *Aequipecten irradians* to metamorphosis, gave only a brief description, but did include in his article a series of photomicrographs showing the different larval stages. His photographs were used later by several other authors.

The smallest normally developed straight-hinge larvae of *Aequipecten irradians* in our cultures measured 80 x 65 μ, and the largest, still unmetamorphosed, swimming individuals were approximately 200 μ long (Figs. 15, 16, 17). Some larvae metamorphosed when they were only about 175 μ long. In general, therefore, the average size of metamorphosing larvae of our scallops closely agrees with that given by Jørgensen (1946) for *Pecten striatus;* but our larvae were considerably smaller, by about 50 μ, than those of another European scallop, *P. opercularis*, which, according to Jørgensen, may be as long as 260 μ.

The larvae appear somewhat asymmetrical at all stages and this condition becomes more pronounced in the advanced stages of development (Fig. 16). A slight notch sometimes is visible at the base of the shells of larvae measuring 125 μ or more. The notch is located on the left, pointed end of the larval shell but generally is not pronounced and is difficult to photograph. This mark may be helpful, however, in identifying live or recently preserved larvae.

In general, scallop larvae are pale and are considerably lighter than most other forms with which we have worked (Loosanoff & Davis, 1963). The color darkens as the larvae grow older, although they still remain relatively transparent.

Most larvae measuring 170 μ or more have an "eye" spot. In larger larvae, however, this spot is difficult to find, possibly because the "eye" is not too well defined and because the shells become thicker. A small, inconspicuous "eye" was noticed in some larvae only 150 μ long.

6. *Ostrea edulis* Linnaeus

We introduced this European oyster in American waters because it propagates at a considerably lower temperature than our eastern oyster, *Crassostrea virginica. Ostrea edulis* can develop gonads and spawn in the waters of our northeastern states, such as Maine, and also along the Pacific coast where normally the water is too cold for the successful propagation of *C. virginica* (Loosanoff, 1951).

Since its introduction in the fall of 1949, *Ostrea edulis* has spawned naturally in the waters of New England and has become firmly established in Maine (Loosanoff, 1955, 1962). The set of *O. edulis* grown from selected parents

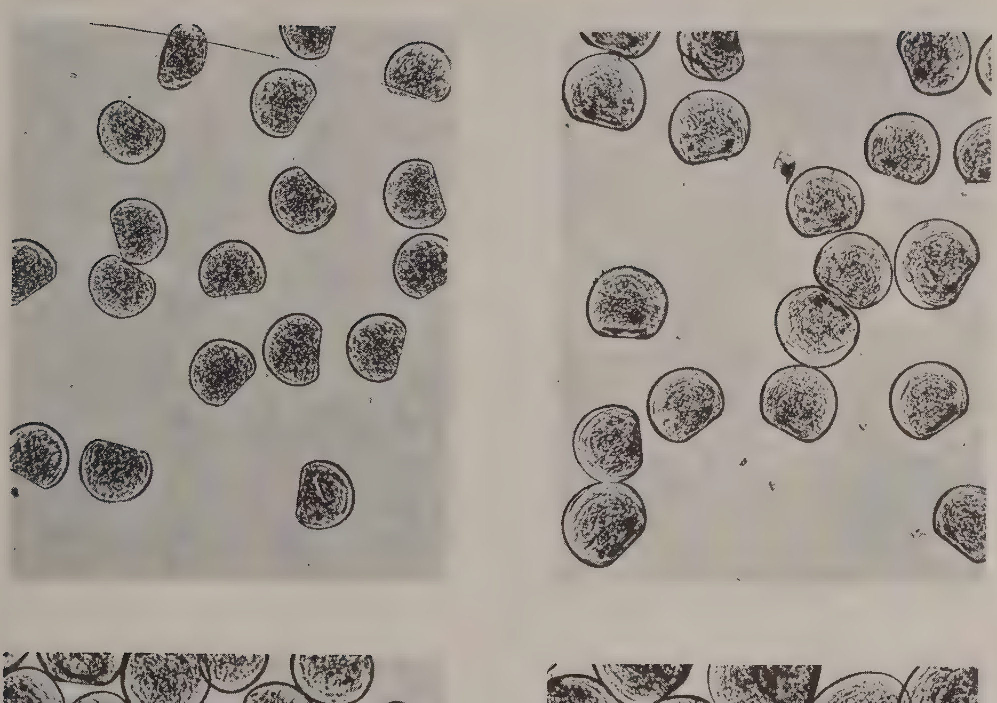


FIG. 15. Group photographs of different sizes of larvae of *Aequipecten irradians*. Smallest individuals of the youngest group are approximately 80 μ long, and the largest of the oldest, approximately 180 μ.

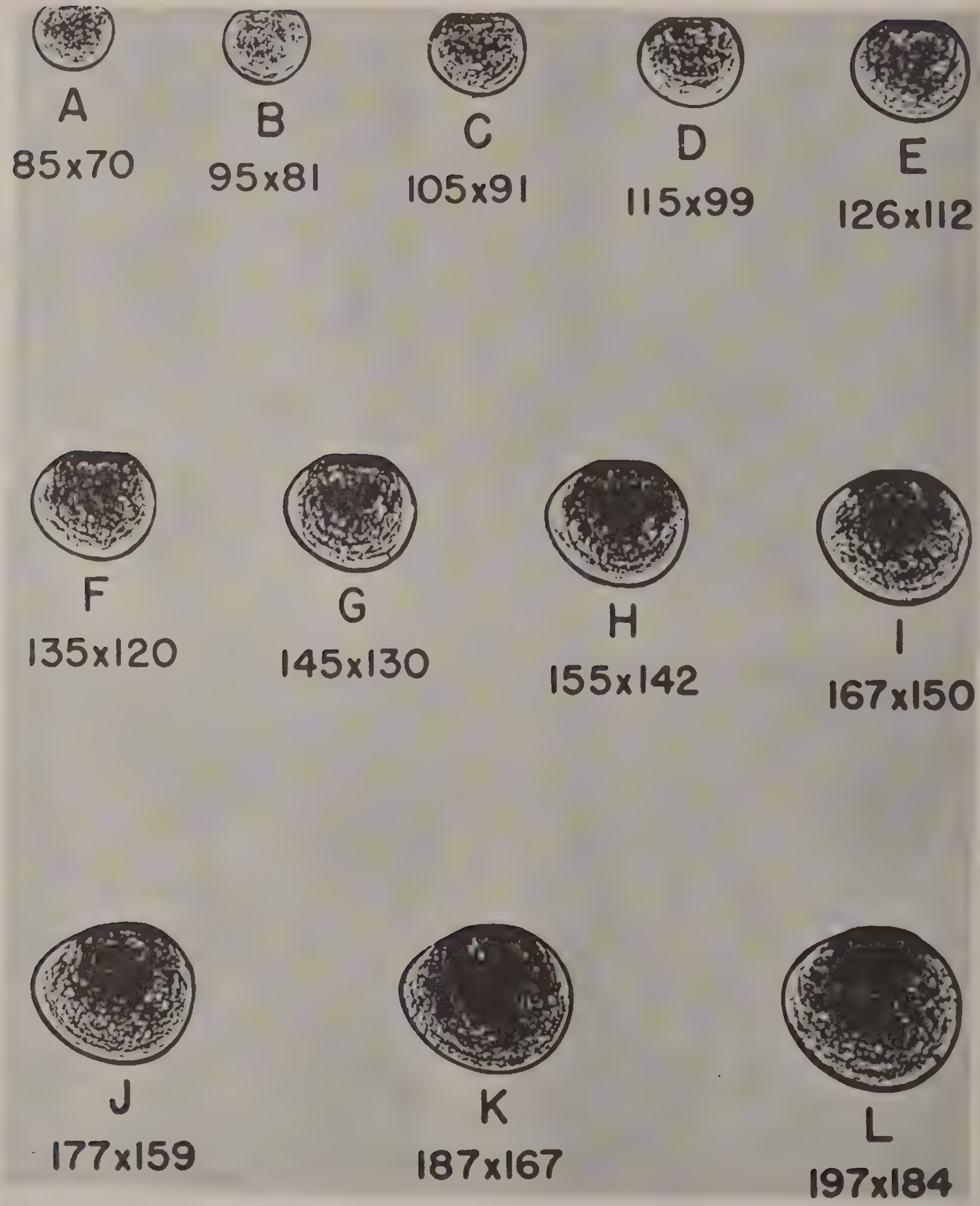

A
85x70
B
95x81
C
105x91
D
115x99
E
126x112
F
135x120
G
145x130
H
155x142
I
167x150
J
177x159
K
187x167
L
197x184

FIG. 16. Photographs of larvae of *Aequipecten irradians* in different stages of development from early straight-hinge stage (A) to the stage of metamorphosis (L). Measurements are in microns; the first figure under a photograph indicates length, and the second, width of the larva.

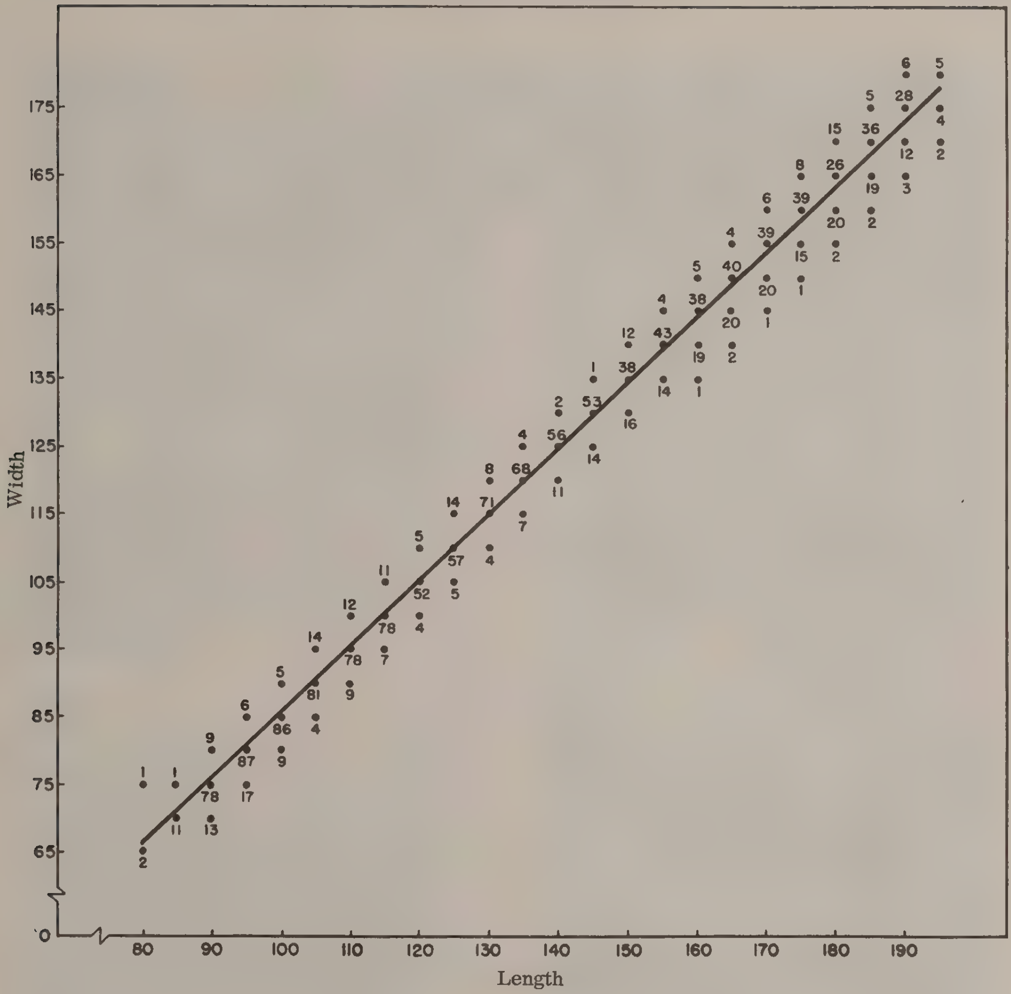


FIG. 17. Length-width relations of larvae of *Aequipecten irradians* during the entire free-swimming veliger stage. Measurements in microns. The figures at dots indicate the numbers of larvae of each dimension.

at the Milford Laboratory was planted in several areas of our Pacific coast. Where it was protected and properly cared for the set grew well. The descendants of the European oysters grew unusually fast in California waters, reaching approximately 4-1/4 inches in about 2 years. They also developed gonads and released larvae in a normal manner. Larvae-bearing *O. edulis* were observed in Tomales Bay, California, in the middle of April.

Those interested in propagation of *Ostrea edulis* should consult reviews by a number of authors, including Orton (1937), Korringa (1941), Walne (1956), Yonge (1960) and Loosanoff & Davis (1963).

Ostrea edulis is a larviparous species which discharges its half-grown larvae into the surrounding water, 6-10 days after spawning, in a process known as

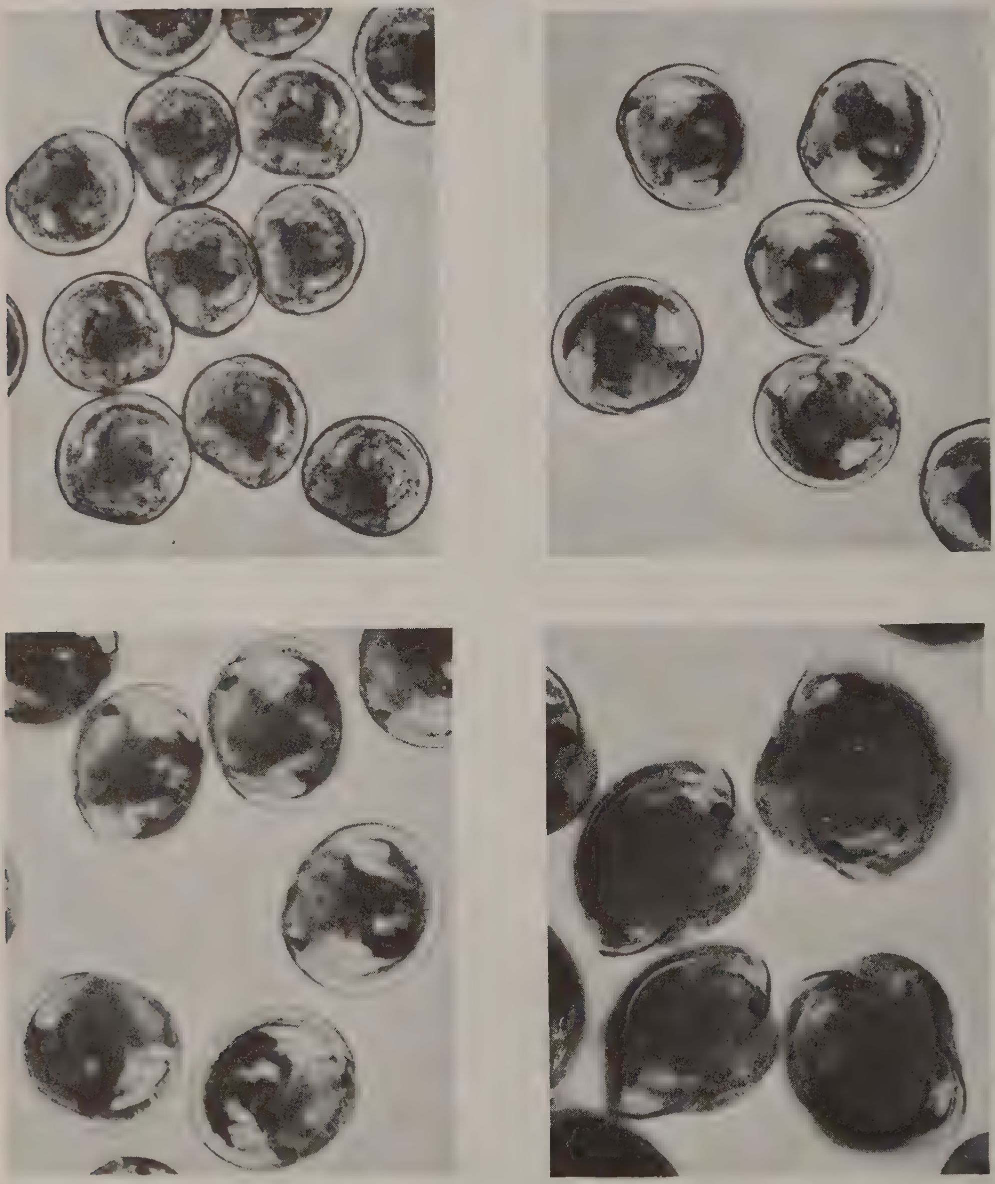


FIG. 18. Group photographs of different sizes of larvae of *Ostrea edulis*. Smallest individuals of the youngest group are approximately 175 μ long, and the largest of the oldest, approximately 300 μ.

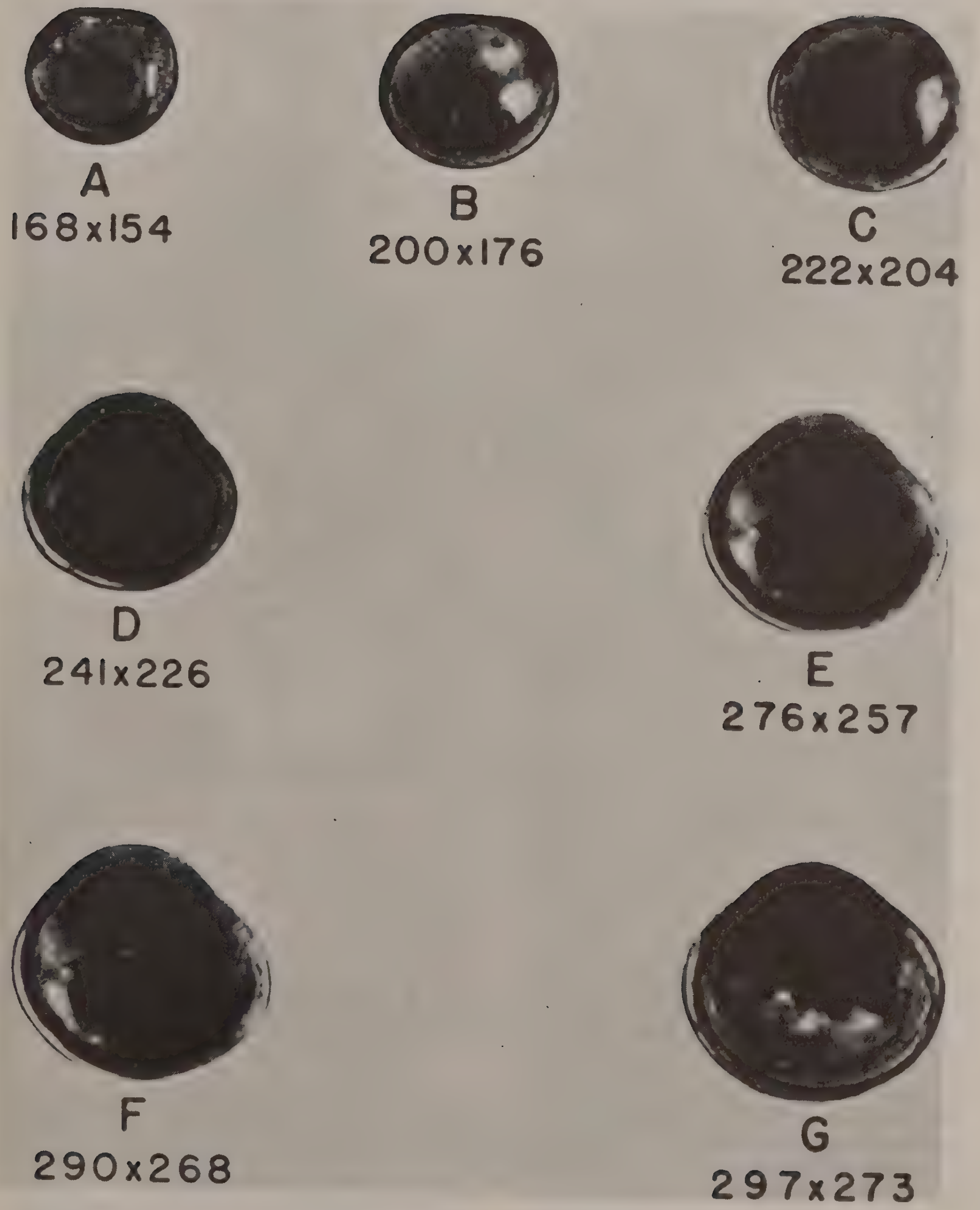

A
168x154
B
200x176
C
222x204
D
241x226
E
276x257
F
290x268
G
297x273

FIG. 19. Photographs of larvae of *Ostrea edulis* from the time they are released in swarming by the parents (A) until the time of metamorphosis (G). Measurements are in microns; the first figure under a photograph indicates length, and the second, width of the larva.

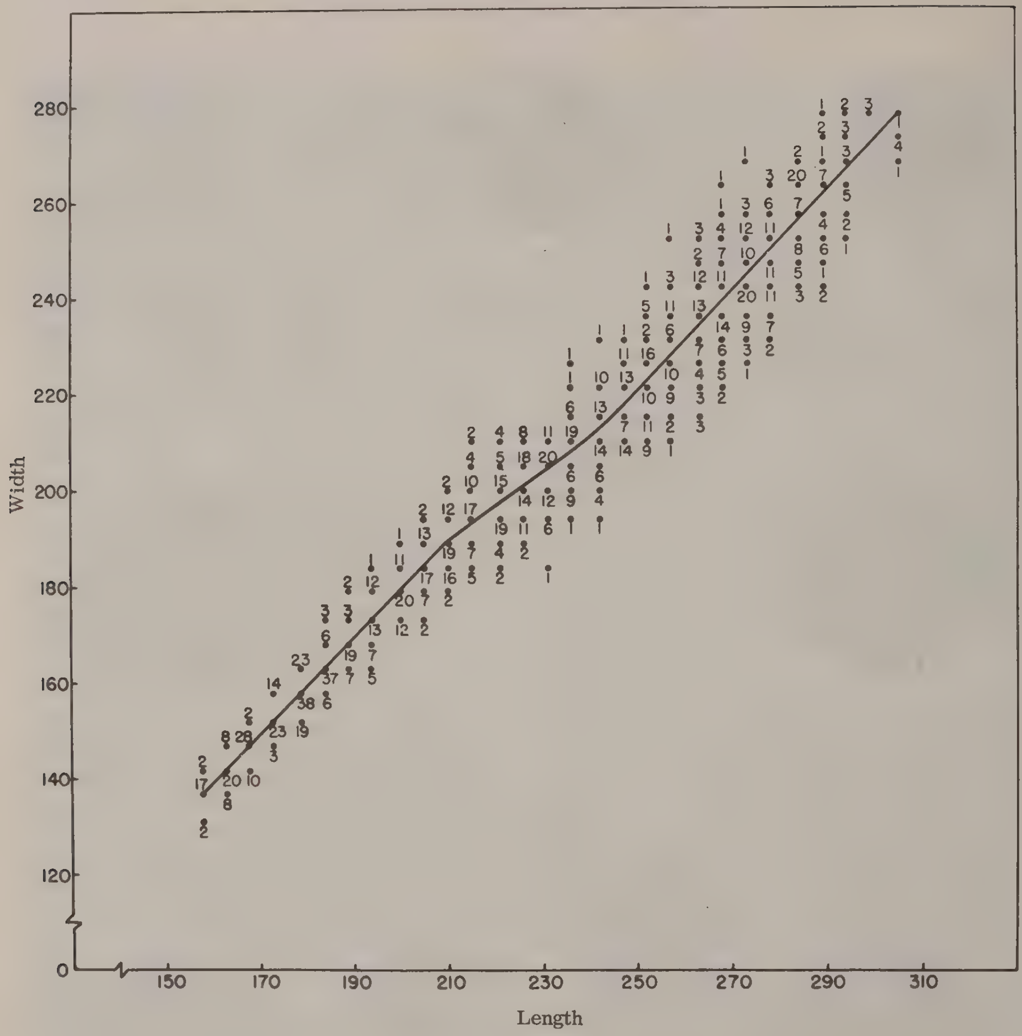


FIG. 20. Length-width relations of larvae of *Ostrea edulis* during the entire free-swimming veliger stage. Measurements in microns. The figures at dots indicate the numbers of larvae of each dimension.

swarming. Until then the fertilized eggs and, later, the larvae are retained in the mantle cavity of the mother oyster. The size of recently released larvae varies considerably even when they are released by the same female at the same swarming (Loosanoff & Davis, 1963). One female, for example, released larvae that ranged from 142 μ to 199 μ in length. The modal size of the larvae released by 6 separately kept females was about 184 μ. We consider, however, that larvae smaller than 160 μ in length are probably discharged prematurely. Larvae over 160 μ are, apparently, sufficiently developed to grow to metamorphosis without difficulty (Figs. 18, 19, 20).

Even recently released larvae of *Ostrea edulis* are considerably darker than those of most other species cultured at our laboratory, with the possible exception of the larvae of *O. lurida*, a close relative of the European oyster. As the size of the larvae increases, their shells become thicker and their color becomes darker, almost completely obscuring the internal organs. Soon after the larvae reach approximately 210 μ the umbo becomes more prominent, and at about 240 μ it is well defined (Fig. 19). Most of the larvae develop a prominently pigmented "eye" spot at 250 μ which, however, cannot be found easily in preserved specimens.

Setting occurred most commonly when the individuals were between 280 μ and 300 μ long. Cole (1936) came to the same conclusions. Nevertheless, we have never seen larvae as large as 350 μ observed by Cole in his cultures. Imai *et al.* (1953a) found that none of the larvae of *Ostrea edulis*, which they cultured under controlled conditions, reached 300 μ. In this respect we are in close agreement with our Japanese colleagues. Walne (1956) also reported that most of the larvae of *O. edulis*, which he reared, metamorphosed before reaching 300 μ.

As can be seen from the length-width relationship in Fig. 20, the median line displays a depression which begins at about 215 μ and persists until the length is approximately 255 μ. A somewhat similar depression is noticed in the median line of the related species, *Ostrea lurida* (Fig. 23).

7. *Ostrea lurida* Carpenter

Ostrea lurida, the native oyster of our Pacific coast, is found from Alaska to lower California. It is a common intertidal form which several decades ago was of considerable commercial importance. It is a close relative of *O. edulis*, the flat European oyster, but is much smaller.

Regardless of the difference in sizes of fully grown individuals of the 2 species, the average length of the normal larvae of *Ostrea lurida* at the time of swarming is about 185 μ, practically the same as that of the larvae of *O. edulis* (Loosanoff & Davis, 1963). Observations of other workers on the sizes of recently discharged larvae of *O. lurida* closely agree with ours (Hori, 1933; Hopkins, 1937; Imai *et al.*, 1954). Relatively small larvae measuring only 160 x 150 μ released in some swarmings at our laboratory (Figs. 21, 22, 23) were apparently immature because they were unable to withdraw the velum completely. Under favorable conditions some of these larvae may survive and finally reach metamorphosis.

Larvae become darker as they grow. Soon after they reach a length of about 205 μ the umbo region becomes more prominent, and larvae measuring 275 μ acquire a somewhat triangular outline (Fig. 22). The length becomes greater than the width as size increases, and at time of setting may exceed the latter by about 20 μ. A comparison of Figs. 19 and 22 shows that larvae of the same sizes of *Ostrea edulis* and *O. lurida* closely resemble each other.

The most common setting size of the larvae grown in our laboratory cultures was about 300 μ, which is not too different from the setting sizes of either the larvae of *Ostrea edulis* or, as we will show later, the larvae of the genus *Crassostrea*. Free-swimming larvae of *O. lurida* measuring more than 310 μ were uncommon and larvae somewhat larger, measuring 325 μ, were rare (Fig. 23). In this respect we agree with Imai *et al.* (1954) who reported that some of their largest larvae measured 328 μ.

As mentioned in the discussion of *Ostrea edulis*, the median line of the length-width relationships of the larvae of *O. lurida* shows a depression in its central portion (Fig. 23).

8. *Crassostrea virginica* (Gmelin)

The American, or eastern oyster, *Crassostrea virginica* (formerly *Ostrea virginica*), is the chief commercial

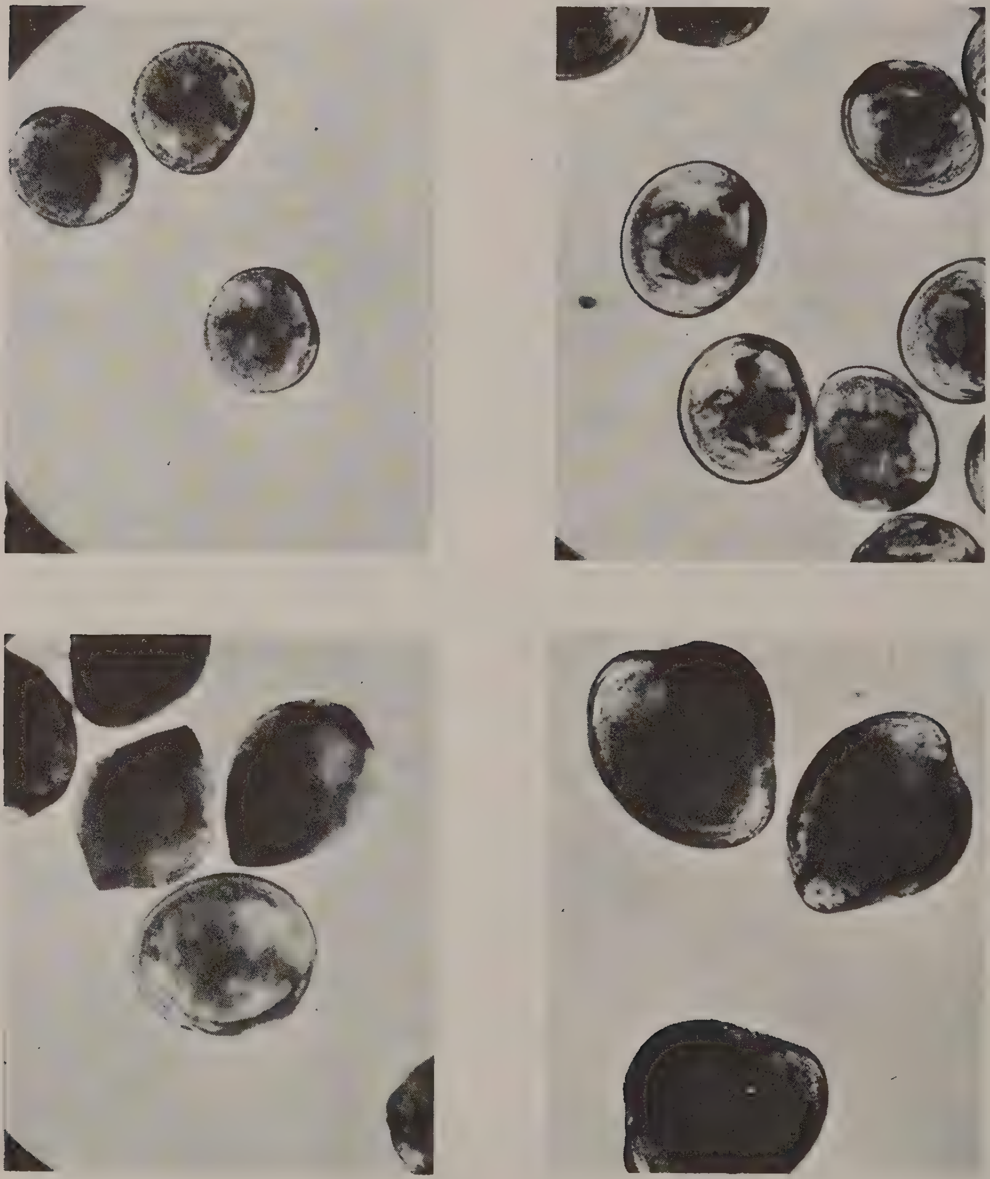


FIG. 21. Group photographs of different sizes of larvae of *Ostrea lurida*. Smallest individuals of the youngest group are approximately 165 μ long, and the largest of the oldest, approximately 295 μ.

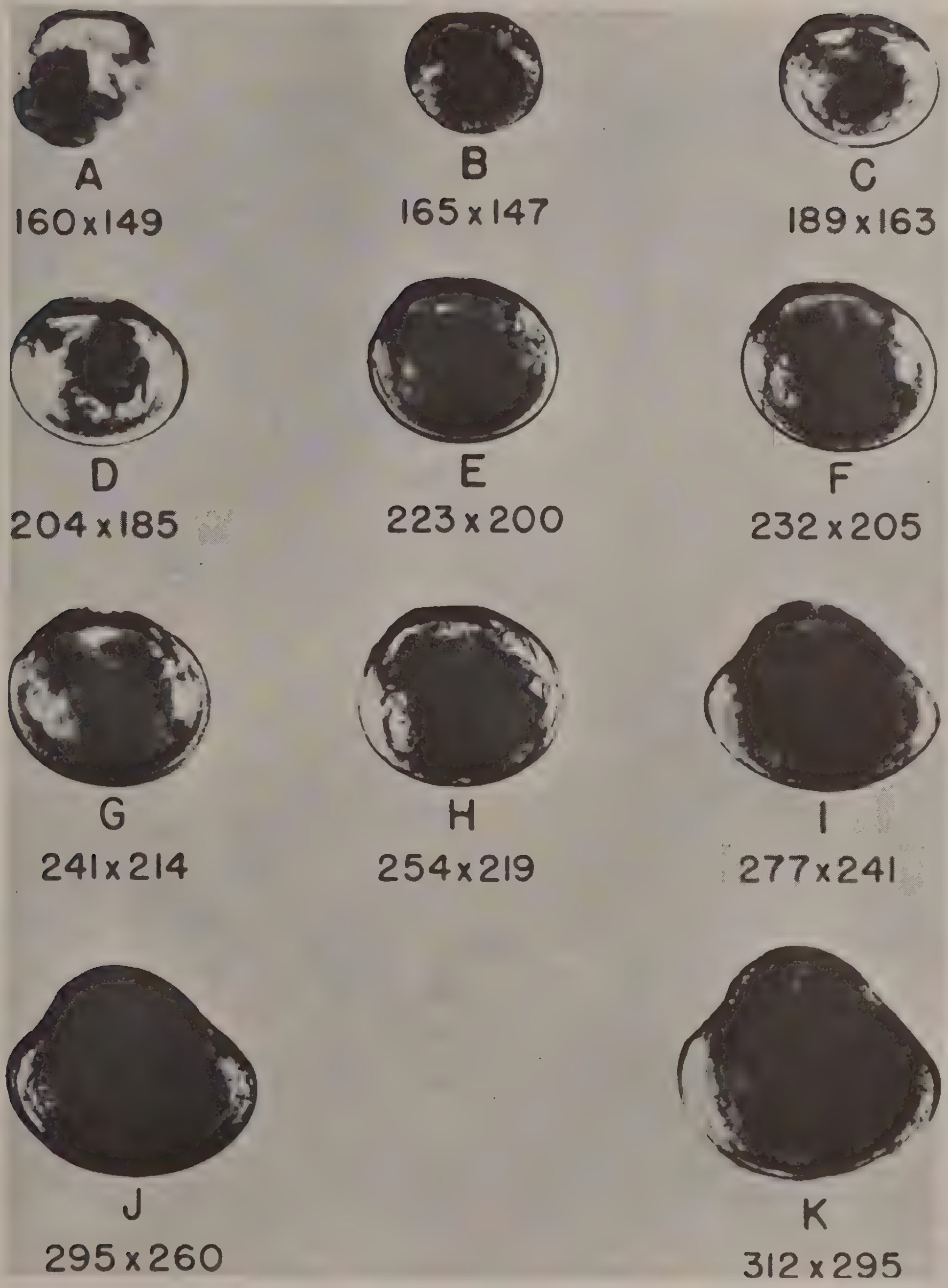

A
160x149
B
165x147
C
189x163
D
204x185
E
223x200
F
232x205
G
241x214
H
254x219
I
277x241
J
295x260
K
312x295

FIG. 22. Photographs of larvae of *Ostrea lurida* from the time they are released in swarming by the parents (A) until the time of metamorphosis (K). Measurements are in microns; the first figure under a photograph indicates length, and the second, width of the larva.

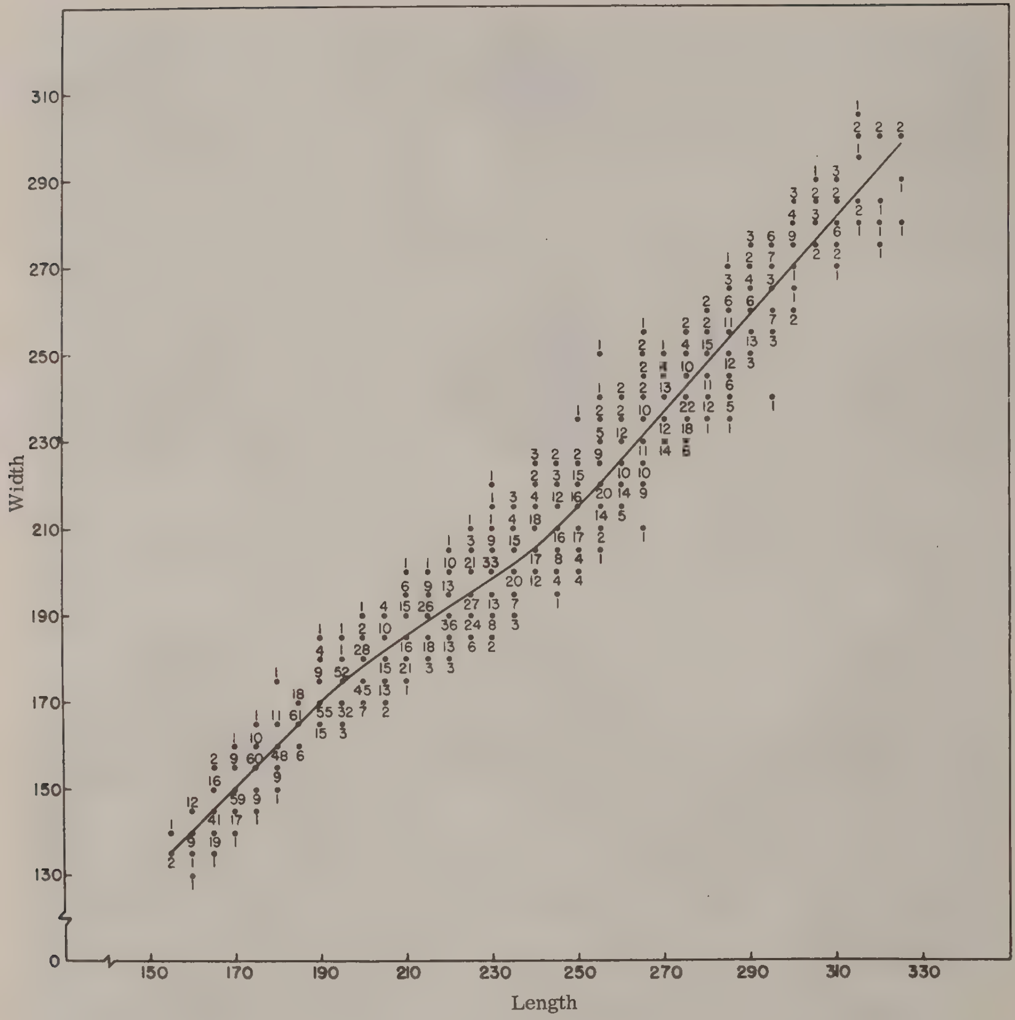


FIG. 23. Length-width relations of larvae of *Ostrea lurida* during the entire free-swimming veliger stage. Measurements in microns. The figures at dots indicate the numbers of larvae of each dimension.

mollusk of our Atlantic and Gulf coasts. It is found in considerable numbers from Massachusetts south along the eastern coast of the United States and also along the Gulf of Mexico. Small groups of this oyster still live in the waters of Maine and New Hampshire. They are also cultivated in Canadian waters, mainly in the southern parts of the Gulf of St. Lawrence. Small quantities are regularly transplanted to several bays of our Pacific coast.

The larvae of *Crassostrea virginica* have been described by many investigators, including Brooks (1880), Stafford (1912), J. Nelson (1909), Churchill (1920), T. Nelson (1921), Wells (1927), Prytherch (1924), Sullivan (1948) and Carriker

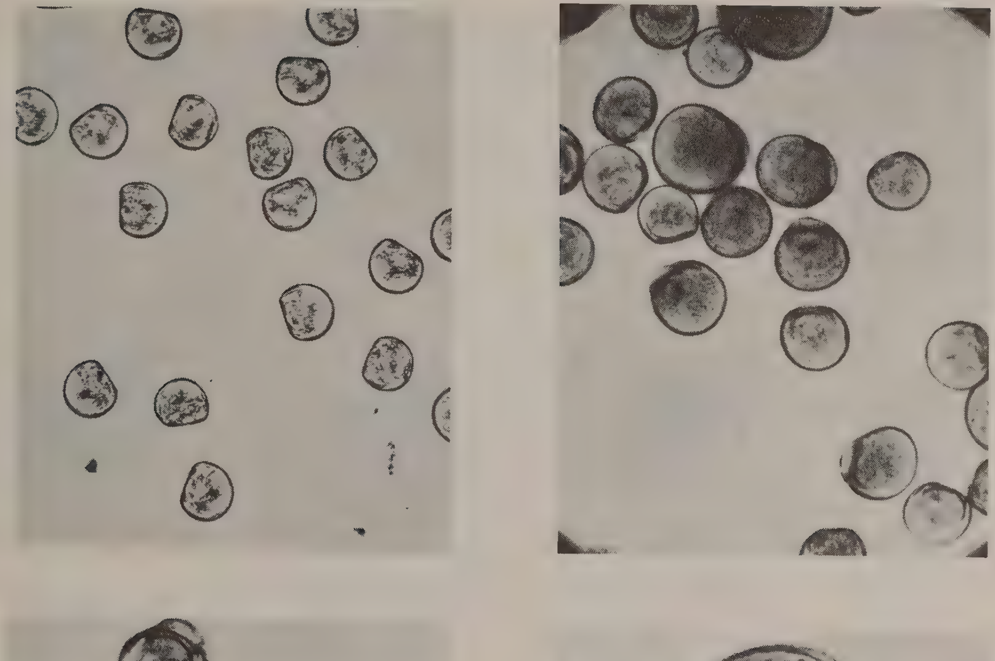


FIG. 24. Group photographs of different sizes of larvae of *Crassostrea virginica*. Smallest individuals of the youngest group are approximately 72 μ long, and the largest of the oldest, approximately 305 μ.

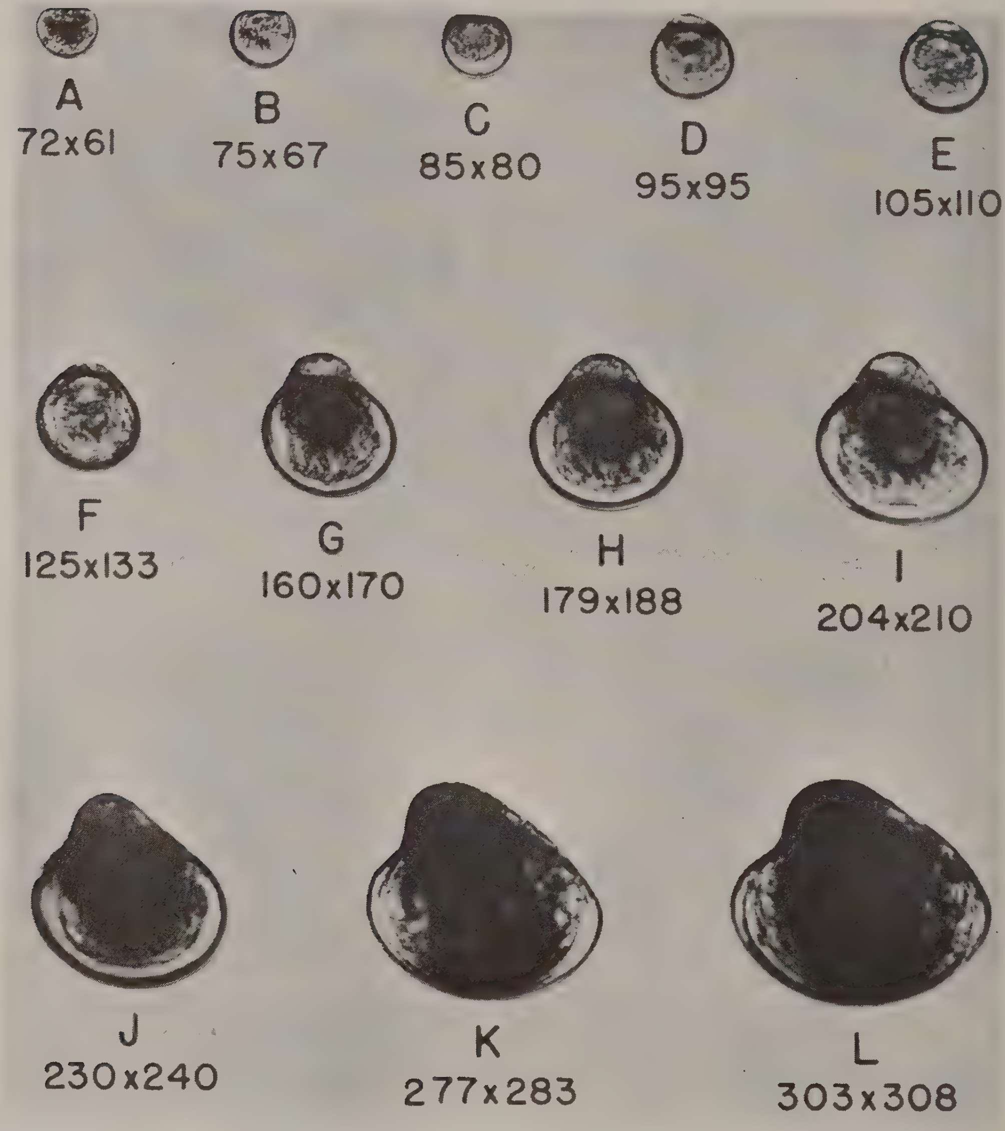

A
72x61
B
75x67
C
85x80
D
95x95
E
105x110
F
125x133
G
160x170
H
179x188
I
204x210
J
230x240
K
277x283
L
303x308

FIG. 25. Photographs of larvae of *Crassostrea virginica* in different stages of development from straight-hinge stage (A) to the stage of metamorphosis (L). Measurements are in microns; the first figure under a photograph indicates length, and the second, width of the larva.

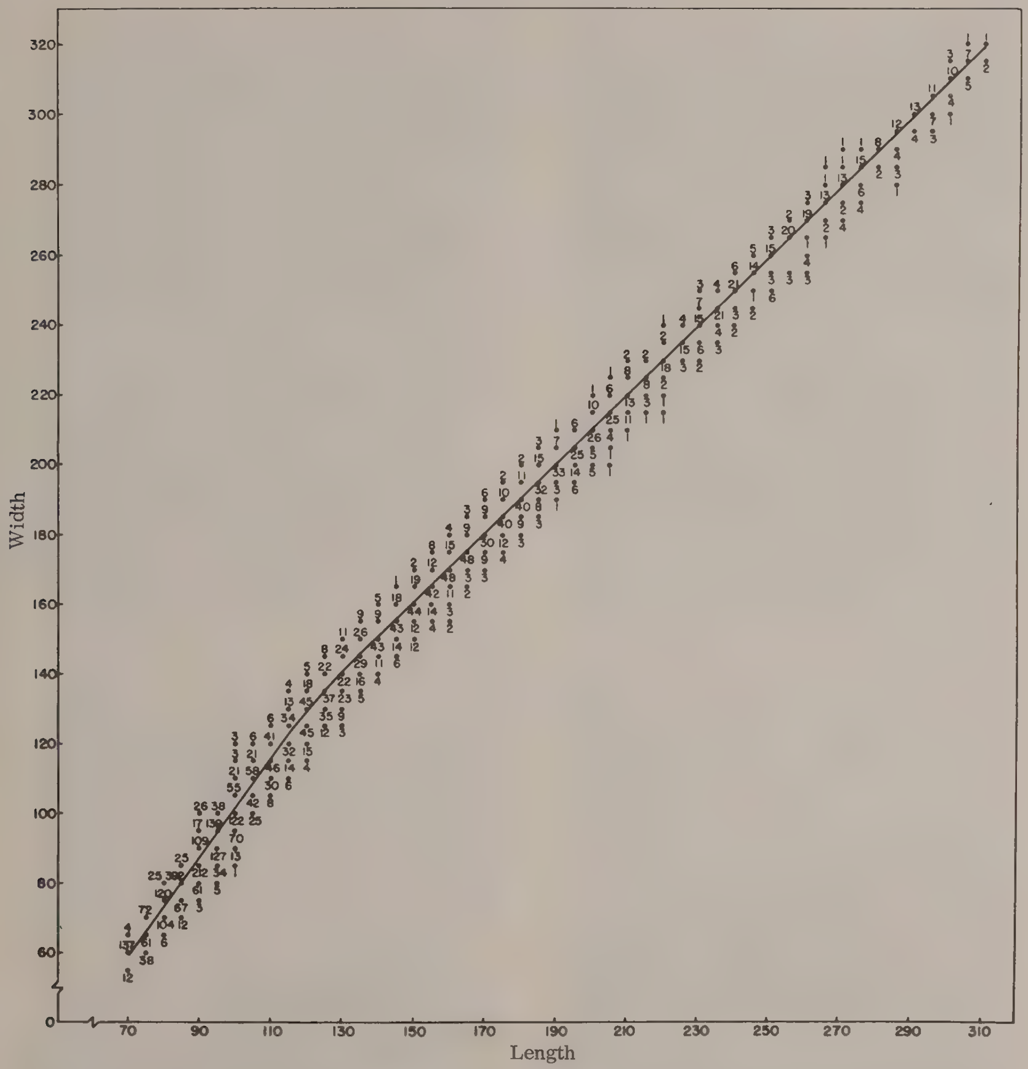


FIG. 26. Length-width relations of larvae of *Crassostrea virginica* during the entire free-swimming veliger stage. Measurements in microns. The figures at dots indicate the numbers of larvae of each dimension.

(1951). Several of these authors offered drawings; J. Nelson (1909) was the first to publish photomicrographs. Later, Wells (1927) and, especially, Sullivan (1948) offered good series of photomicrographs of larvae of different sizes. The larvae shown in the photographs of other investigators, however, were mostly either in straight-hinge stage or near metamorphosis. Yonge (1960) included in his book a series of photomicrographs identical to those in our Fig. 25, which we sent him.

Considerable information on many aspects of the physiology, ecology and growth of the larvae of *Crassostrea* *virginica* was given by Loosanoff & Davis (1963). Their observations show that the smallest normal straight-hinge larvae of *C. virginica*, grown under laboratory conditions, measure about 68 x 55 μ. Usually, however, these larvae are about 75 x 67 μ (Figs. 24, 25, 26). Until the larvae are about 85 μ, their length is normally 5-10 μ greater than their width. The length and width become almost identical, however, at approximately 100 μ. After that stage the increase in width is somewhat more rapid than in length.

The length-width relationship of oyster larvae is almost linear, with the exception of the part representing the length between 105 μ and 130 μ, where the line curves slightly (Fig. 26). It is shown later that *C. gigas*, another member of the genus *Crassostrea*, shows the same curvature in its length-width median line (Fig. 29).

In general, the color of both laboratory-grown and plankton-collected larvae changes with length from golden brown to deeper brown, to almost black when the larvae approach metamorphosis. An umbo begins to form when the larvae are between 85 and 90 μ long and becomes increasingly prominent as they grow larger. The umbo is one of the most pronounced characters of *Crassostrea virginica* larvae (Figs. 24, 25). The pronounced asymmetry of the umbones is an important feature of all larvae that are more than 115 μ long. The asymmetry is due to the much faster development of the left umbo, which eventually becomes so pronounced that it almost obscures the right umbo.

The majority of our laboratory-grown larvae began to metamorphose at lengths between 275 and 315 μ. Some larvae as long as 355 μ were still swimming actively. These observations are in agreement with those on sizes of larvae in plankton samples collected in Long Island Sound during the 30-year period of our observations on spawning and setting of oysters, and also with the measurements of Prytherch (1924), who has done much research on setting of oysters in the same area. The measurements given by Sullivan (1948) also resemble ours, whereas the measurements of Stafford (1912), who gave the maximum size of mature larvae as between 345 and 393 μ, are much greater. Moreover, we disagree with Stafford's measurements of the larvae of smaller sizes, especially within the length range from 105 to 210 μ. In this range Stafford's larvae measure, as a rule, much more in length than in width. This relation does not hold generally (Fig. 25).

9. *Crassostrea gigas* (Thunberg)

This oyster, formerly known as *Ostrea gigas*, is the most important commercial mollusk of Japanese waters. It was introduced to this country around the turn of the century and is now grown in the waters of Washington and California and to a limited extent in Oregon. It is also cultivated in British Columbia.

Because of the comparatively low water temperatures along our Pacific coast, *Crassostrea gigas* does not reproduce regularly there. As a result, the industry depends mainly upon seed oysters imported every spring from Japan. Nevertheless, these oysters spawn occasionally in some comparatively shallow, well-protected waters, and at times their larvae are abundant in plankton. Sets of commercial importance have occurred in certain areas.

The larvae of *Crassostrea gigas* have been studied extensively by many Japanese workers. These studies were reviewed by Cahn (1950) and Imai *et al.* (1950b). Our studies of larvae of *C. gigas* (Figs. 27, 28, 29) show that they are actually identical in size and appearance to the larvae of *C. virginica*. The length of the youngest well-formed straight-hinge larvae was approximately 70 μ, and the size at metamorphosis was near 300 μ. Regardless of the similarity of the 2 species, as far as size and shape of larvae were concerned, efforts to cross these 2 forms failed (Davis, 1950; Imai *et al.*, 1950b). Our observations on the sizes of *C. gigas* closely agree with those of our Japanese

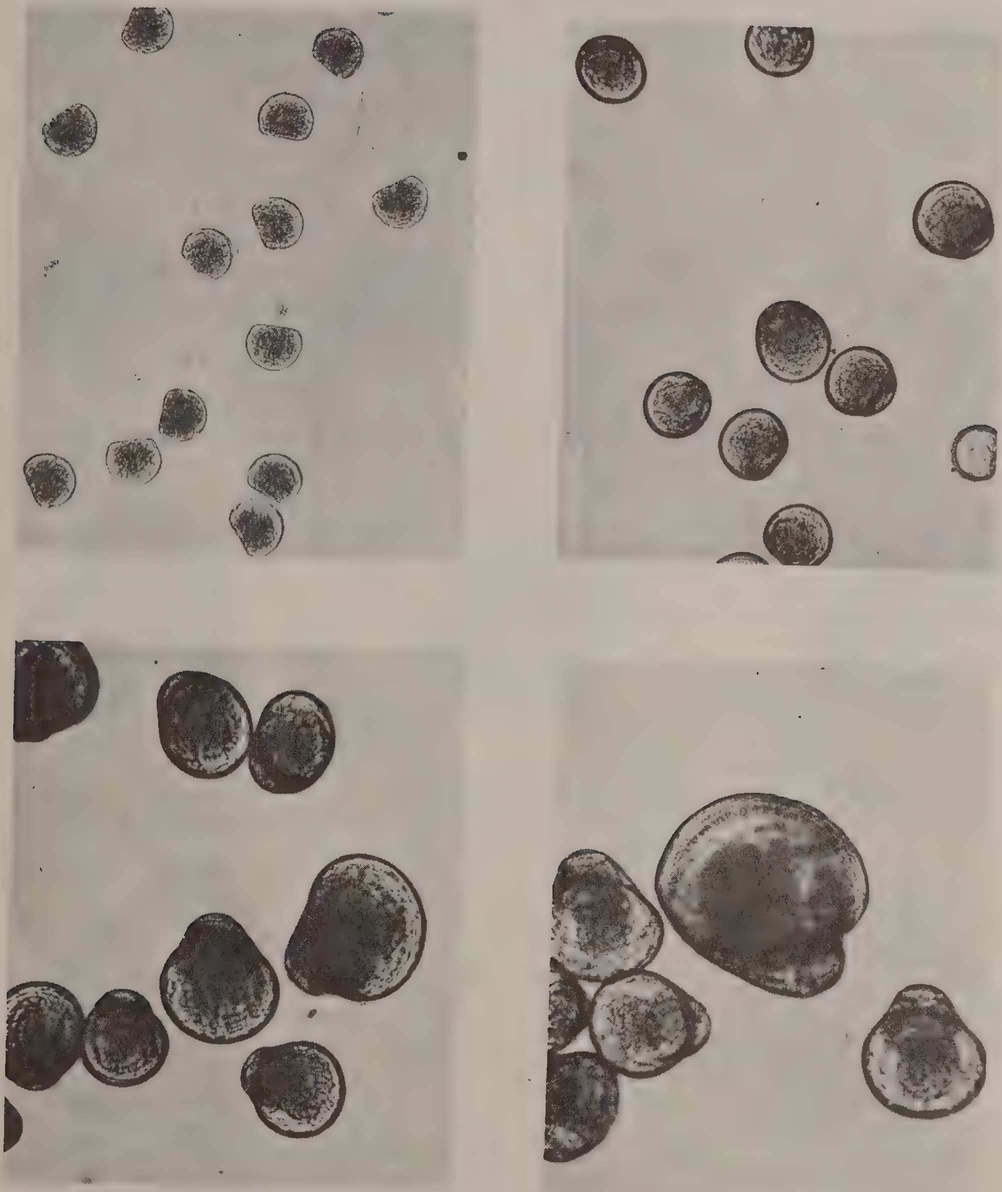


FIG. 27. Group photographs of different sizes of larvae of *Crassostrea gigas*. Smallest individuals of the youngest group are approximately 70 μ long, and the largest of the oldest, approximately 285 μ.

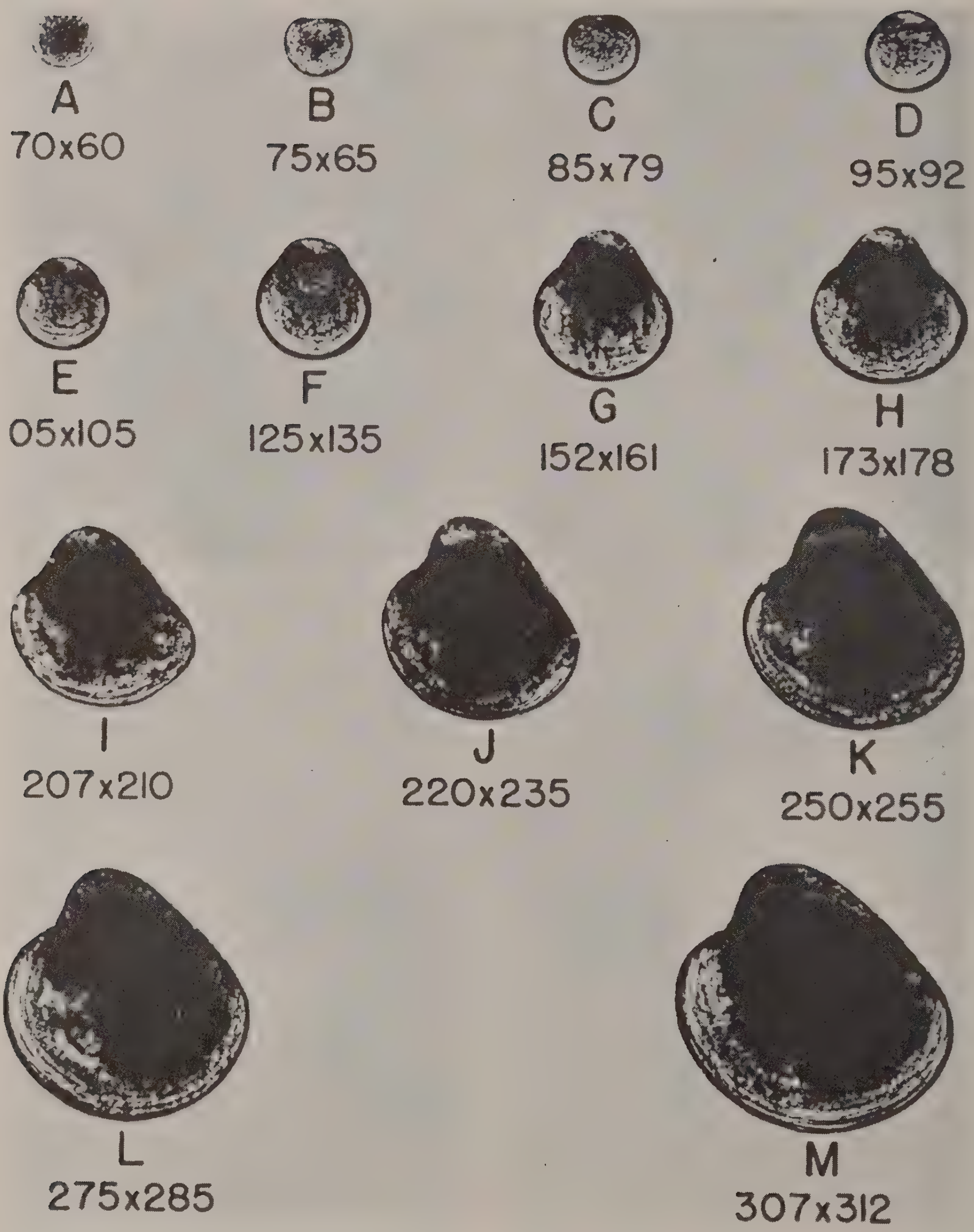

A
70x60
B
75x65
C
85x79
D
95x92
E
05x105
F
125x135
G
152x161
H
173x178
I
207x210
J
220x235
K
250x255
L
275x285
M
307x312

FIG. 28. Photographs of larvae of *Crassostrea gigas* in different stages of development from early straight-hinge stage (A) to the stage of metamorphosis (M). Measurements are in microns; the first figure under a photograph indicates length, and the second, width of the larva.

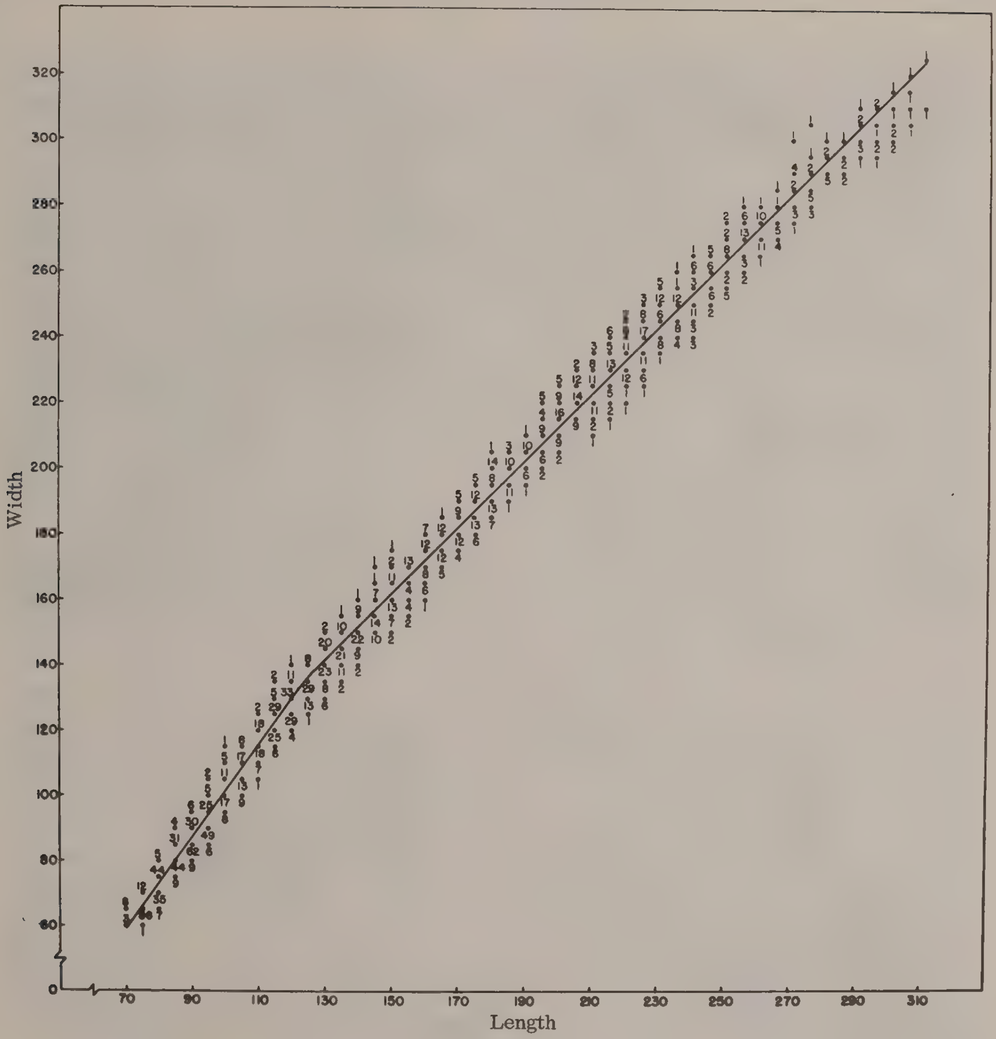


FIG. 29. Length-width relations of larvae of *Crassostrea gigas* during the entire free-swimming veliger stage. Measurements in microns. The figures at dots indicate the numbers of larvae of each dimension.

colleagues, including Hori & Kusakabe (1926) and Imai et al. (1950b).

Tanaka (1954), from studies of *Crassostrea gigas* from widely separated oyster beds of Japan, concluded that the length of the prodissoconch of this oyster at the time of metamorphosis varied with locality. It was smaller in the northern areas and increased along the southern parts of the Japanese coast.

10. *Mercenaria* (=*Venus*) *mercenaria* (Linnaeus)

One of the most important commercial clams of our Atlantic coast, *Mercenaria mercenaria*, is known by many names, including Round clam, Hardshell clam and quahog. It is found from the

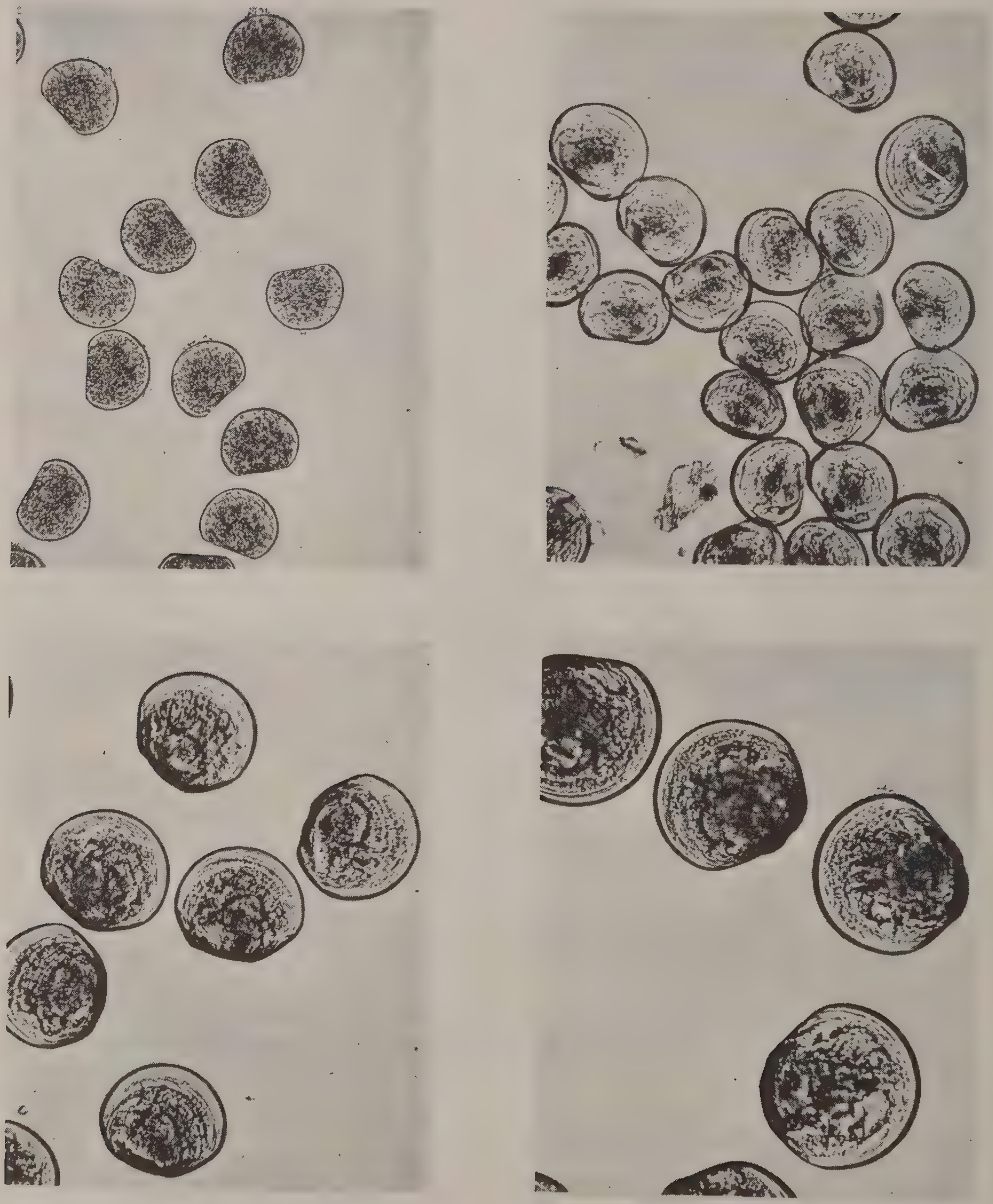


FIG. 30. Group photographs of different sizes of larvae of *Mercenaria mercenaria*. Smallest individuals of the youngest group are approximately 101 μ long, and the largest of the oldest, approximately 210 μ.

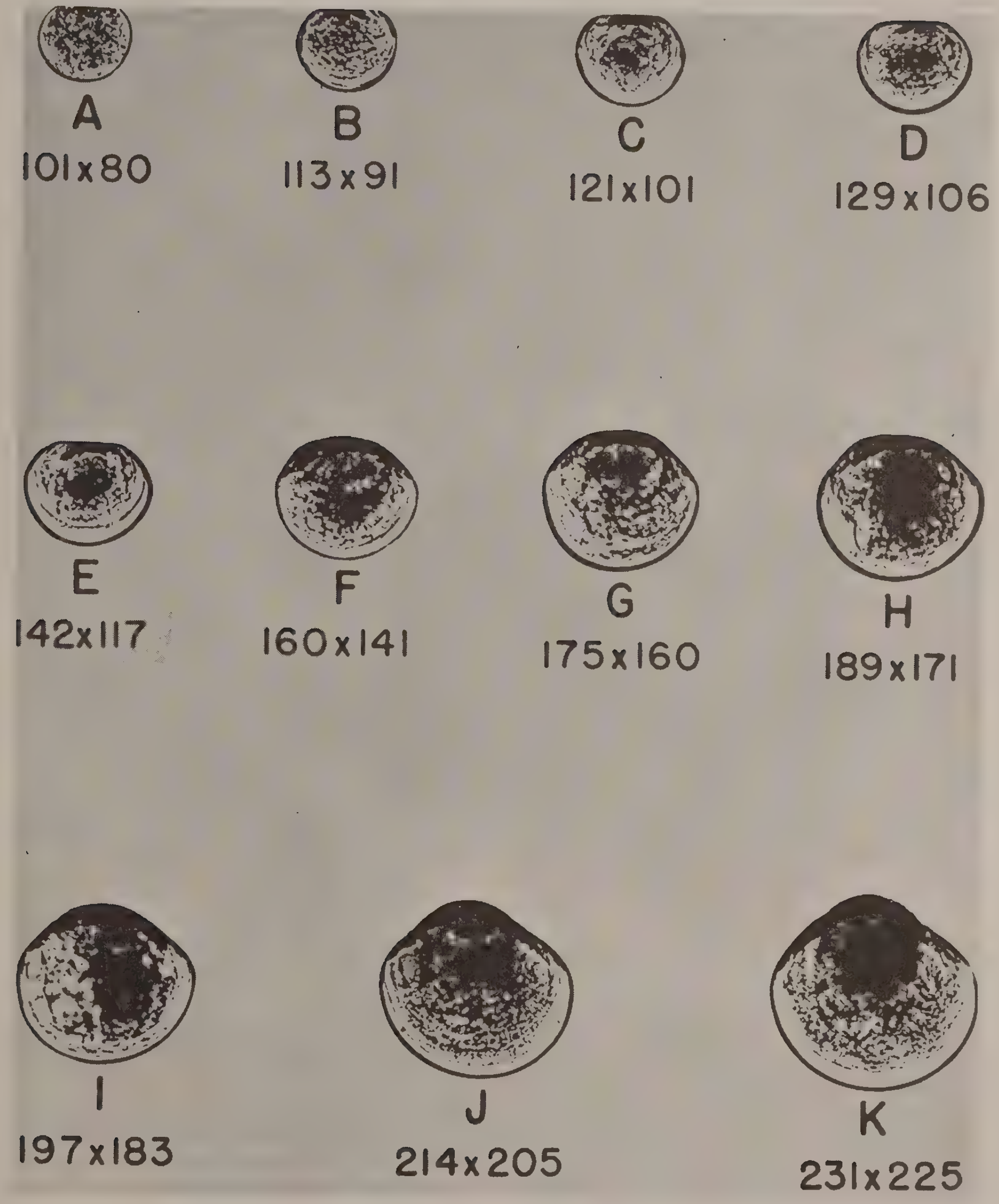

A
101x80
B
113x91
C
121x101
D
129x106
E
142x117
F
160x141
G
175x160
H
189x171
I
197x183
J
214x205
K
231x225

FIG. 31. Photographs of larvae of *Mercenaria mercenaria* in different stages of development from early straight-hinge stage (A) to the stage of metamorphosis (K). Measurements are in microns; the first figure under a photograph indicates length, and the second, width of the larva.

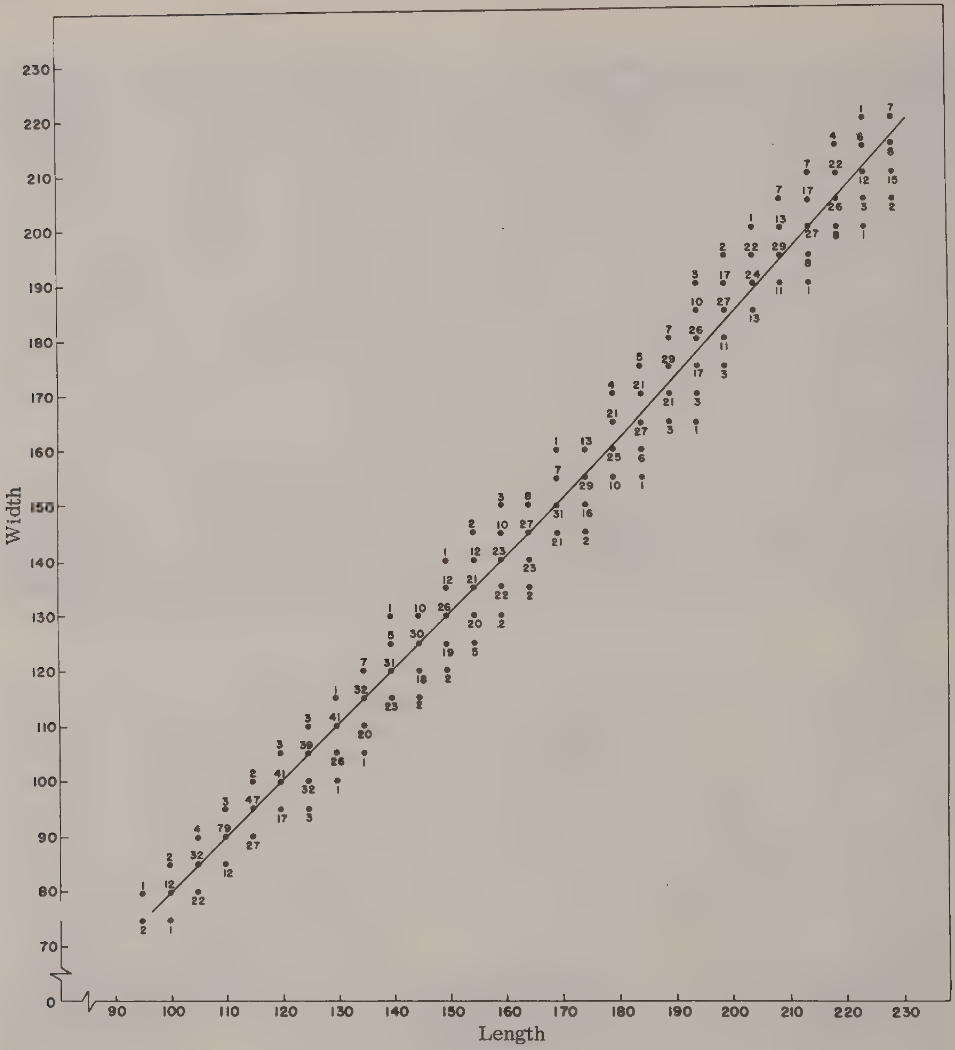


FIG. 32. Length-width relations of larvae of *Mercenaria mercenaria* during the entire free-swimming veliger stage. Measurements in microns. The figures at dots indicate the numbers of larvae of each dimension.

Gulf of St. Lawrence to Texas and is especially common south of Cape Cod.

The larvae of this clam have been described and illustrated by several investigators, including Stafford (1912), Belding (1912), Wells (1927), Sullivan (1948) and Carriker (1961). Until the larvae could be cultured from known parents under laboratory conditions, however, there was no assurance that the descriptions were really of this species. The first information of this nature was offered by Loosanoff & Davis (1950), who included in their article photomicrographs and measurements of the larvae from their early straight-hinge stage to metamorphosis. Later, many other investigators, including Turner & George

(1955) and Carriker (1961), cultured the larvae successfully. Because of the numerous recent studies of larvae of this species no uncertainty exists as to their general appearance and dimensions (Loosanoff & Davis, 1963).

In our laboratory cultures only a few straight-hinge larvae were less than 100 μ long and most fully formed, straight-hinge veligers were approximately 105 x 80 μ (Figs. 30, 31, 32). Carriker (1961) also recorded comparatively small larvae, some of which were only 98 x 78 μ.

An umbo becomes visible when the larvae reach the length of approximately 125-130 μ (Figs. 30, 31). As the larvae continue to grow, their umbones become better defined but they are never as prominent as in such other bivalves as *Anomia*, *Crassostrea* and *Teredo*. Some larvae begin to metamorphose when they are only about 170 μ long. The most common length at metamorphosis is between 200 and 215 μ. Larvae 230 μ long or longer are uncommon. At metamorphosis, length is only 5-15 μ greater than width. Carriker (1961) reported that the largest clam veligers of Little Egg Harbor, New Jersey, ranged from 182-198 μ; thus, they metamorphosed at the same size as the larvae of *Mercenaria mercenaria* of Long Island Sound.

We disagree with Stafford's (1912) report indicating that the larvae of *Mercenaria mercenaria* grow to the size of 448 μ before setting. Sullivan (1948) also described larvae of a species other than *M. mercenaria*, because she reported the maximum size of the larvae as 320 μ, which is considerably larger than the size of fully mature larvae of this species. Sullivan later explained (personal communication) that she had confused larvae of *M. mercenaria* with those of another bivalve. Jørgensen (1946) found that metamorphosing veligers of the closely related species, *Venus gallina*, vary from 210-225 μ in length, a size similar to ours.

More recently, Ansell (1961, 1962) gave a comprehensive account of the appearance and functional morphology of the closely related species, *Venus gallina* (=*V. striatula*). According to Ansell the larvae of this species metamorphosed at approximately the same size as the larvae of *Mercenaria mercenaria*. Ansell cultured the larvae from known parents and under controlled conditions.

We have grown the larvae of *Mercenaria mercenaria* from parents from widely separated geographical areas, but size of larvae at metamorphosis did not differ in different groups. Moreover, the larvae reared at 5 different temperatures metamorphosed at about the same size.

11. *Mercenaria* (=*Venus*) *campechiensis* (Gmelin)

This clam, known as the southern quahog and closely related to *Mercenaria mercenaria*, is found on the Atlantic coast from Chesapeake Bay to Florida. Large numbers are also found in the Gulf of Mexico.

The larvae used in our studies originated from parents brought from the sandy beaches of Apalachicola, Florida, in the Gulf of Mexico. All stages of the larvae were identical to similar stages of *Mercenaria mercenaria* (Figs. 33, 34, 35). The lengths of early straight-hinge veligers ranged from 100-110 μ. Metamorphosis occurred most commonly within the length range of 175-215 μ.

As was already reported (Loosanoff & Davis, 1963), the spawning behavior of these 2 species was also virtually the same. Their larvae, when grown under identical conditions, including temperature, grew at the same rate and began to metamorphose at the same time and the same size. These observations contradict the conclusion (Thorson, 1950) that the eggs and larvae of the southern species, when grown at a certain temperature, develop more slowly than those of the northern species of the same genus. Reciprocal crosses of the 2 species produced viable larvae which grew to metamorphosis. These hybrids were fertile and their larvae were

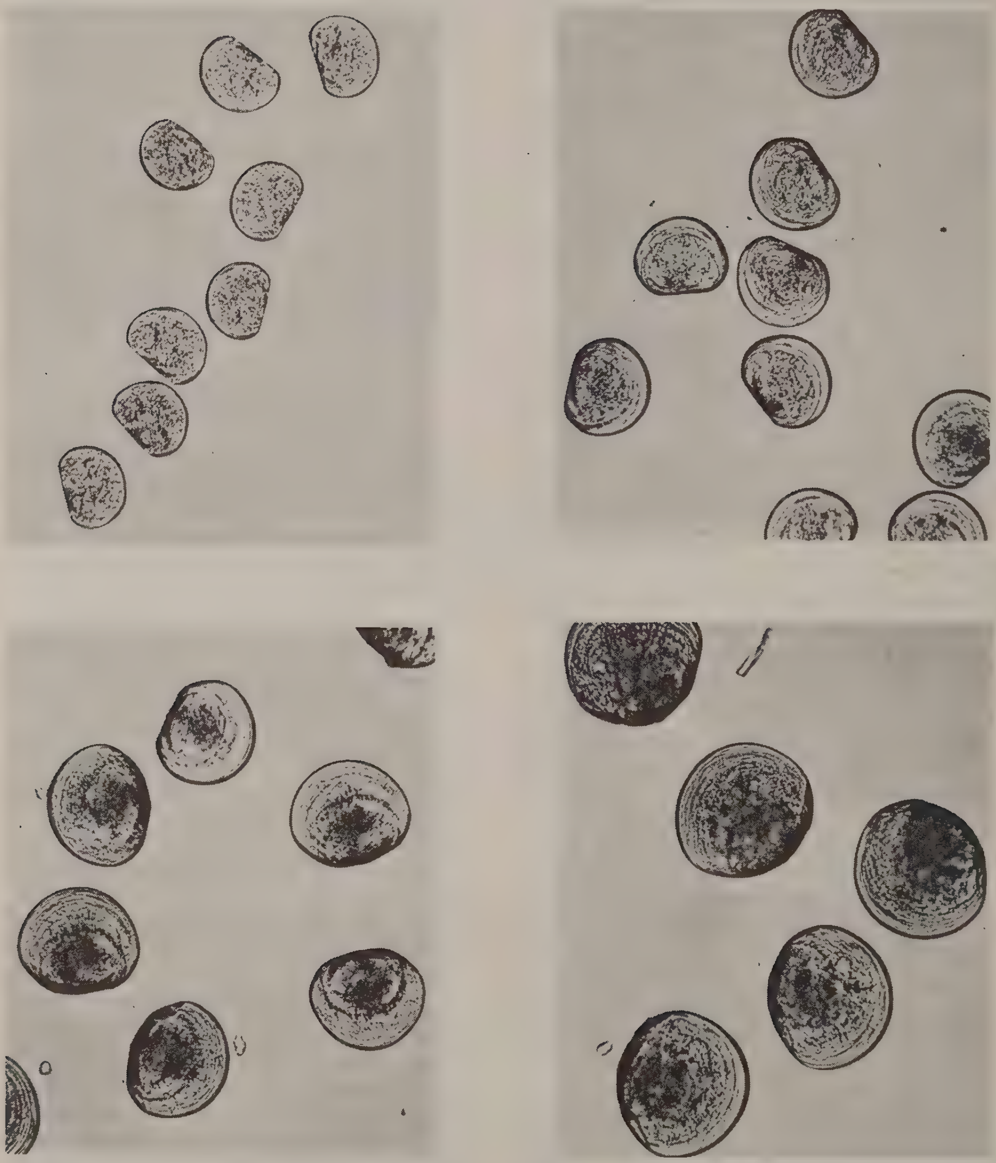


FIG. 33. Group photographs of different sizes of larvae of *Mercenaria campechiensis*. Small-individuals of the youngest group are approximately 100 μ long, and the largest of the oldest, approximately 185 μ.

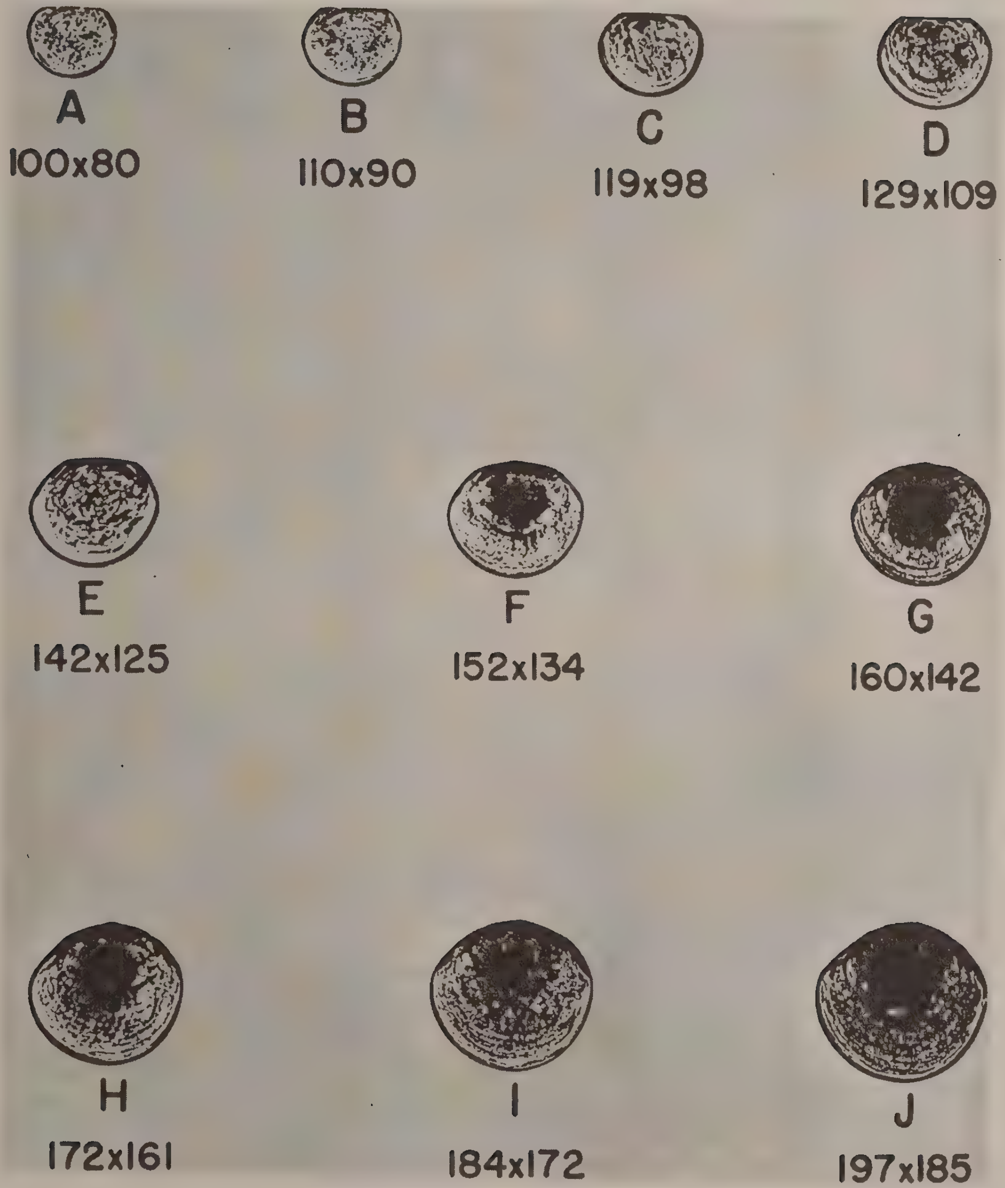

A
100x80
B
110x90
C
119x98
D
129x109
E
142x125
F
152x134
G
160x142
H
172x161
I
184x172
J
197x185

FIG. 34. Photographs of larvae of *Mercenaria campechiensis* in different stages of development from early straight-hinge stage (A) to the stage of metamorphosis (J). Measurements are in microns; the first figure under a photograph indicates length, and the second, width of the larva.

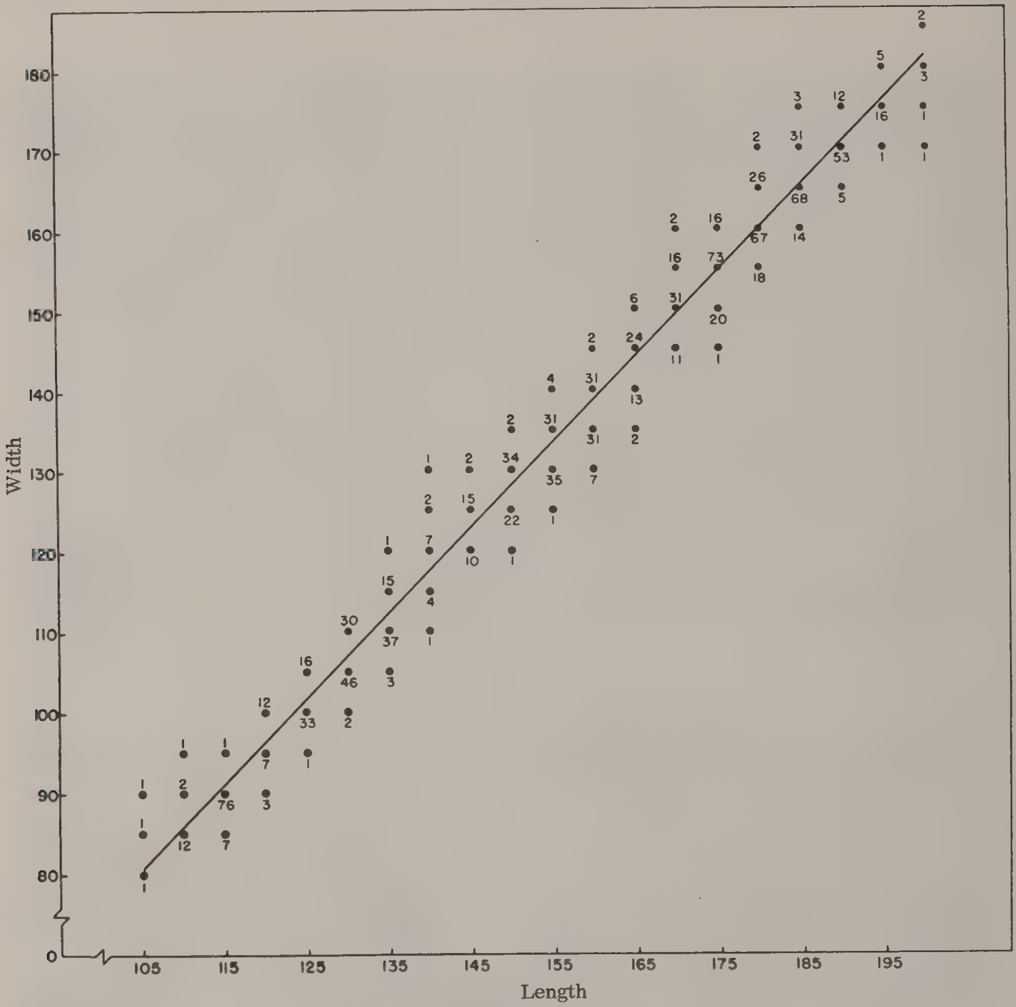


FIG. 35. Length-width relations of larvae of *Mercenaria campechiensis* during the entire free-swimming veliger stage. Measurements in microns. The figures at dots indicate the numbers of larvae of each dimension.

reared to adult stage.

We have seen no publications describing the dimensions or shapes of larvae of *Mercenaria campechiensis* or any aspects of the behavior.

12. *Mulinia lateralis* (Say)

This little clam occurs along the Atlantic coast from Canada to Mexico and is known by a variety of names, including Duck clam, Little Surf clam, Coot clam and sometimes Small Mactra. In some years *Mulinia lateralis* is common in Long Island Sound, both below and above low-water mark. They are usually found in the first half-inch of the bottom.

Larvae of this clam are extremely numerous in plankton samples, especially during the latter part of the summer. The smallest straight-hinge larva, a single animal, recorded in the cul-

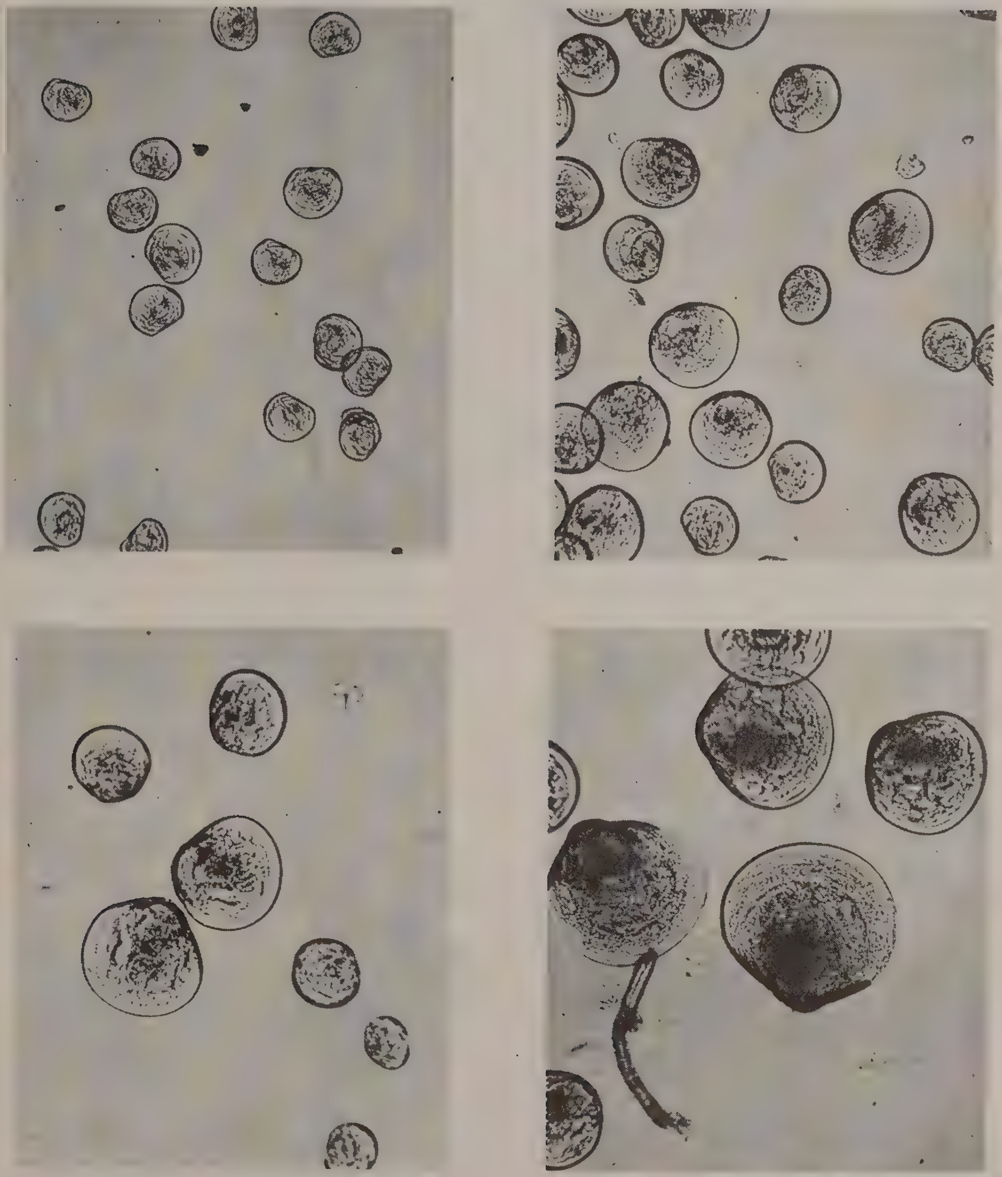


FIG. 36. Group photographs of different sizes of larvae of *Mulinia lateralis*. Smallest individuals of the youngest group are approximately 60 μ long, and the largest of the oldest, approximately 225 μ.

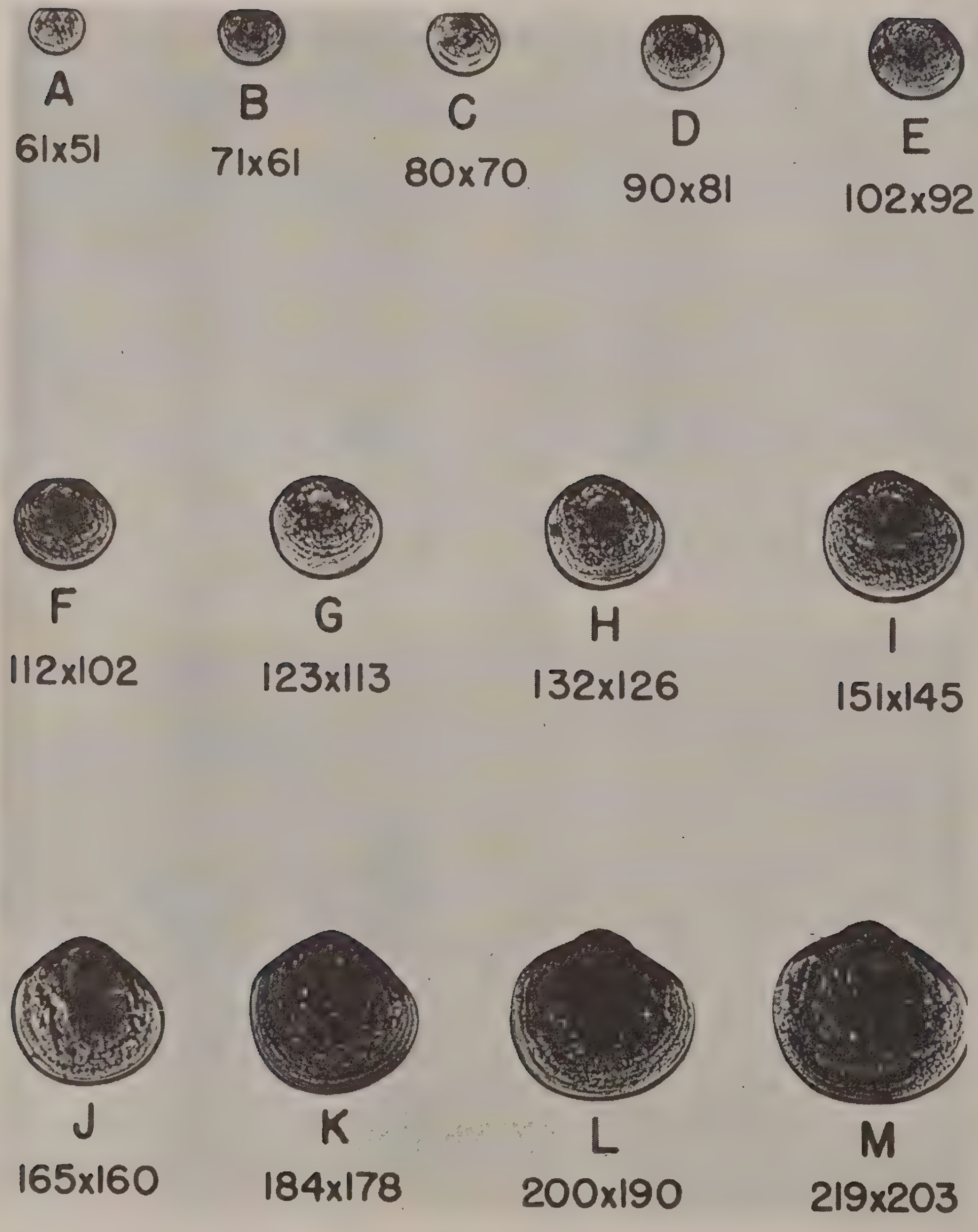

A
61x51
B
71x61
C
80x70
D
90x81
E
102x92
F
112x102
G
123x113
H
132x126
I
151x145
J
165x160
K
184x178
L
200x190
M
219x203

FIG. 37. Photographs of larvae of *Mulinia lateralis* in different stages of development from early straight-hinge stage (A) to the stage of metamorphosis (M). Measurements are in microns; the first figure under a photograph indicates length, and the second, width of the larva.

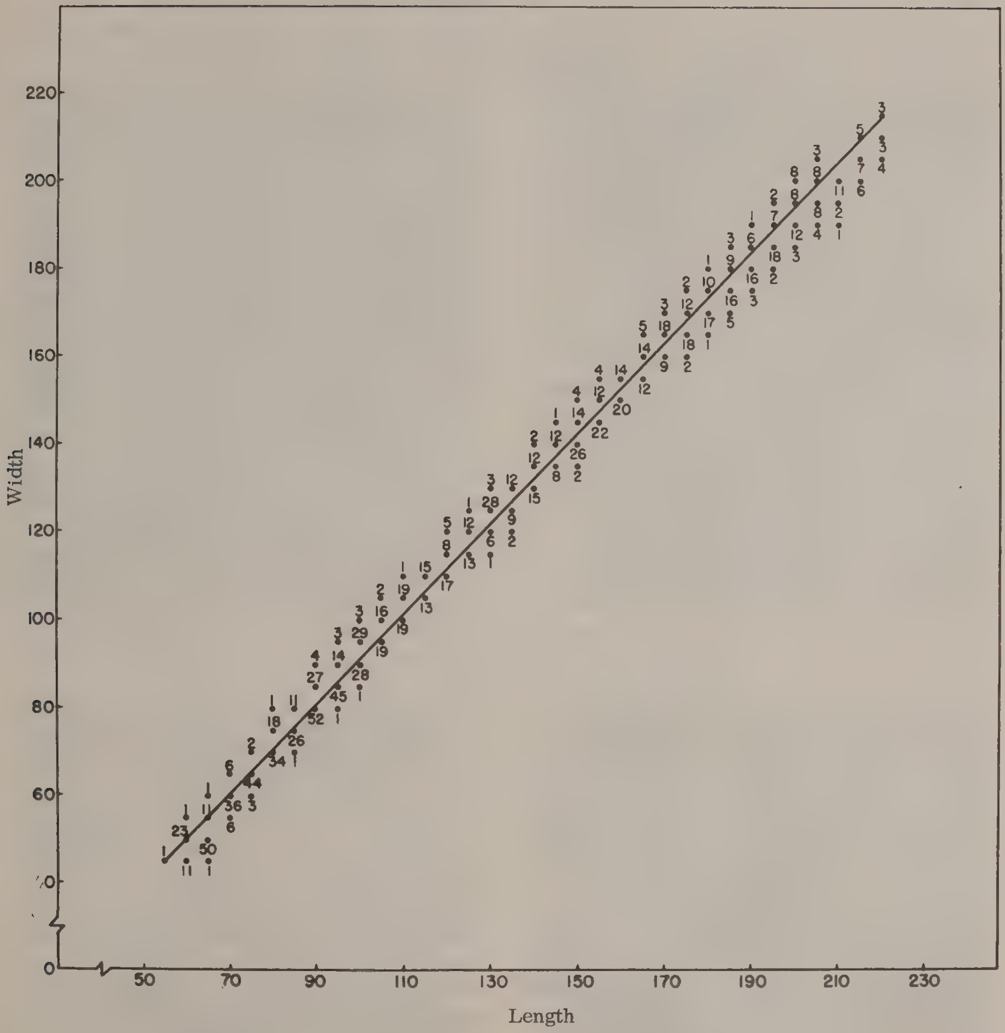


FIG. 38. Length-width relations of larvae of *Mulinia lateralis* during the entire free-swimming veliger stage. Measurements in microns. The figures at dots indicate the numbers of larvae of each dimension.

tures grown at our laboratory was only 55 μ long by 44 μ wide. Normal young straight-hinge larvae measure about 60 x 50 μ (Figs. 36, 37, 38). As is common among lamellibranch larvae, the widths of individuals of the same length vary considerably. For example, the widths of larvae 60 μ long may vary from 45-55 μ.

The early stages of *Mulinia lateralis* larvae, although somewhat smaller, closely resemble those of *Crassostrea virginica*. After the larvae reach the length of about 105 μ, however, their general appearance becomes distinctly different from oyster larvae; their umbones are much less pronounced than in the larvae of *C. virginica* of the same size.

Most larvae undergo metamorphosis at lengths from 210-230 μ. Variation is considerable, however, because some individuals as small as 190 μ appeared entirely metamorphosed, whereas others as large as 235 μ were still swimming. Measurements of the prodissoconch portion of the shell of spat measuring 250-350 μ in length showed that the prodissoconchs ranged from 215-222 μ. These figures agree closely with the measurements of the average sizes of larvae approaching metamorphosis in our cultures. Width is usually about 10 μ less than the length throughout most of the developmental period but it may be 20-25 μ smaller in larvae more than 200 μ long. No evidence of "eye" spot or other distinctive marks was found in larvae as they approached setting.

Sullivan (1948) is the only author who offered descriptions and a series of photomicrographs of the larvae of *Mulinia lateralis*. The size range of her larvae, however, differed significantly from ours. Her minimum size, 85 x 75 μ, is about 25 μ larger than the young straight-hinge larvae recorded in our cultures. Her maximum size, 270 x 245 μ, exceeded the size of our largest larvae by about 35 μ. Sullivan stated further that the straight-hinge larvae were pale yellow and that their color became more intense, changing to a bright yellow as the larvae grew. We found that the young larvae are usually silvery and transparent, not yellow, and that even the old larvae do not become bright yellow.

13. *Tapes semidecussata* Reeve

This clam, accidentally introduced into the State of Washington with seed of *Crassostrea gigas* imported from Japan, is now common along our Pacific coast from Canada to California. In Japan it is one of the most important commercial species of clams (Cahn, 1951). In this country it is called the Japanese little neck, or Manila clam. It appears in literature under many names, including *Tapes japonica*, *Venerupis semidecussata*, *V. philippinarum* and *Paphia philippinarum*. Some authors, such as Quayle (1952), have preferred to use the generic name *Venerupis* instead of *Paphia* or *Tapes*. Abbott (1954), whom we follow, used *Tapes*.

Although some smaller individuals were seen occasionally in our cultures, fully formed, straight-hinge larvae were usually about 95 x 70 μ (Figs. 39, 40, 41). Throughout the larval development, widths of the larvae were about 15-25 μ less than the lengths. The umbo began to form at a length of about 120 μ and became prominent when the larvae were about 140 μ long (Fig. 40). In older larvae the umbones were somewhat more pronounced than in *Mercenaria mercenaria* but, in general, the larvae of *Tapes semidecussata* and *Mercenaria mercenaria* closely resemble each other, especially in the early straight-hinge stage.

The smallest larvae undergoing metamorphosis were about 175 μ long, but most of them metamorphosed at 200-220 μ. Occasionally, individuals as large as 235 μ were swimming and displayed a prominent, functional velum.

Yoshida (1953) gave the dimensions of fully grown veligers of *Venerupis* (=*Tapes*) *semidecussata* as 200 x 190 μ. These measurements agree with our observations on the dimensions of larvae at which metamorphosis may occur. Later, Yoshida (1960, 1964), working with *Tapes variegata*, which is probably the same form as *T. semidecussata*, reported that fully grown veligers measured from about 200 x 180 μ to 215 x 200 μ. Quayle (1952) gave the size of a mature larva of *Venerupis* (=*Tapes*) *pullastra* as 260 x 240 μ, about 25 μ longer than the largest swimming larvae we observed in our cultures. Rees (1950), who placed this species in the genus *Paphia*, gave the size of the mature prodissoconch as 240 μ, which is not much greater than our free-swimming larvae (Fig. 41).

14. *Pitar* (=*Callocardia*) *morrhuana* Gould

This species is found on our Atlantic coast from Prince Edward Island to Cape Hatteras. Its general appearance resembles that of *Mercenaria mercenaria* but it is considerably smaller and has a

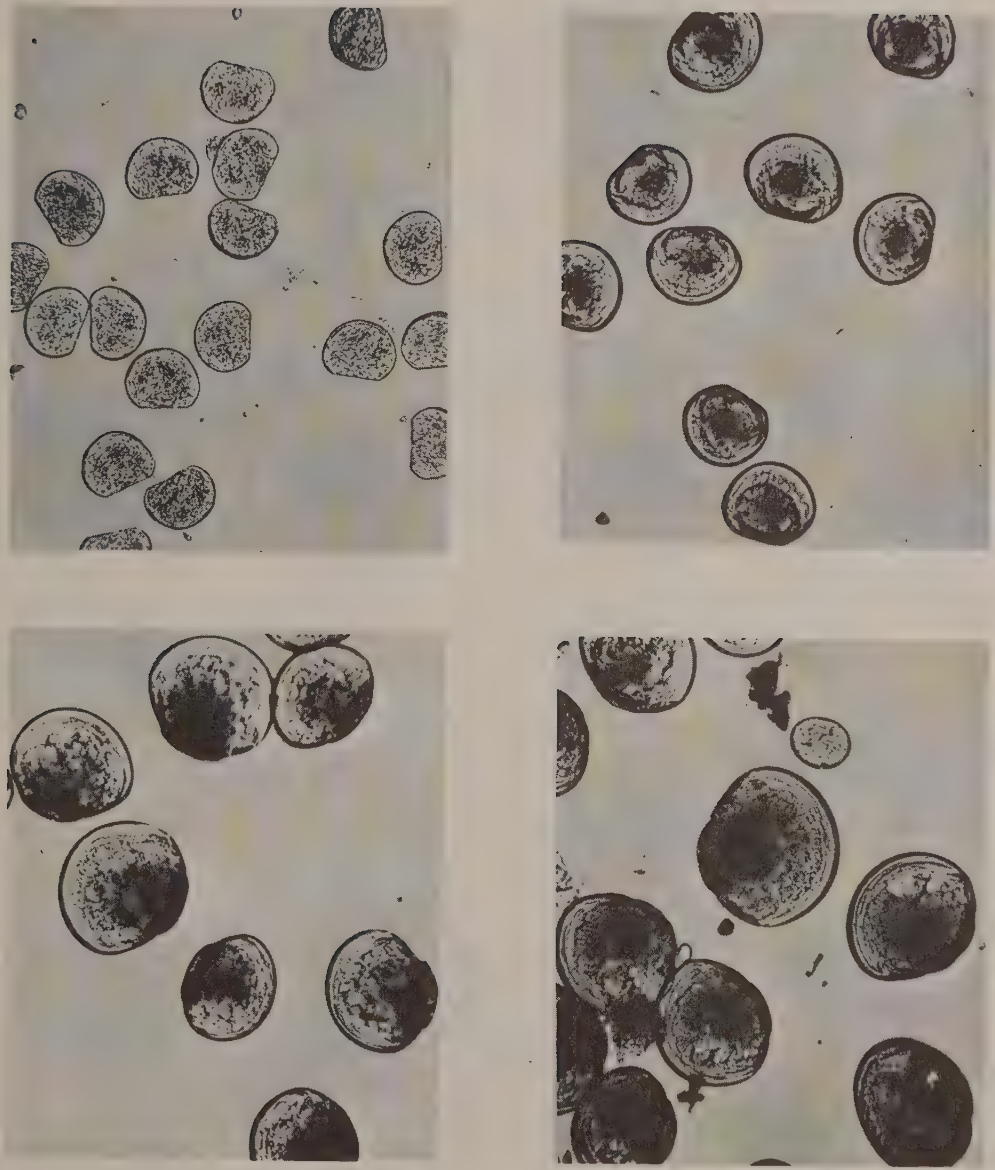


FIG. 39. Group photographs of different sizes of larvae of *Tapes semidecussata*. Smallest individuals of the youngest group are approximately 93 μ long, and the largest of the oldest, approximately 215 μ.

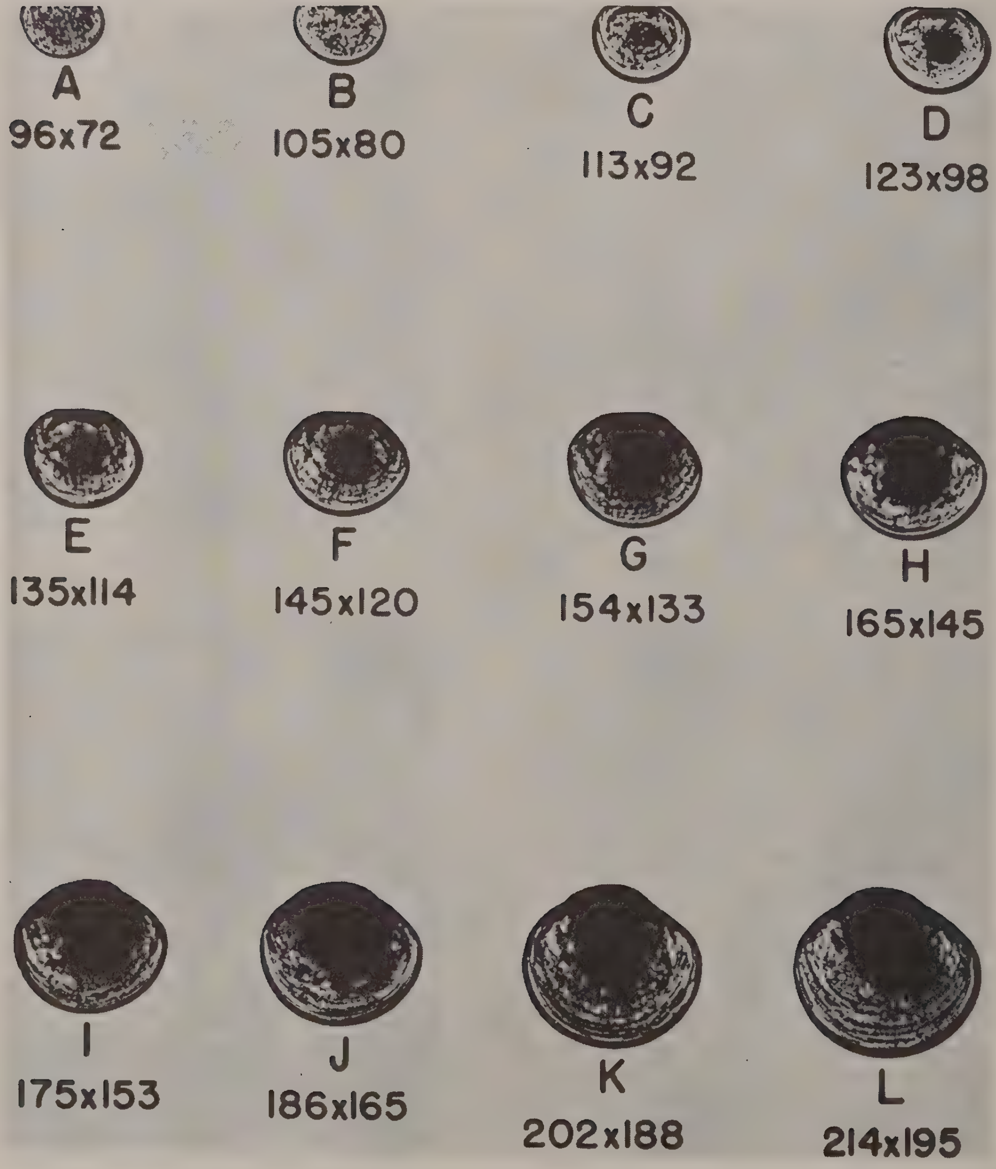

A
96x72
B
105x80
C
113x92
D
123x98
E
135x114
F
145x120
G
154x133
H
165x145
I
175x153
J
186x165
K
202x188
L
214x195

FIG. 40. Photographs of larvae of *Tapes semidecussata* in different stages of development from early straight-hinge stage (A) to the stage of metamorphosis (L). Measurements are in microns; the first figure under a photograph indicates length, and the second, width of the larva.

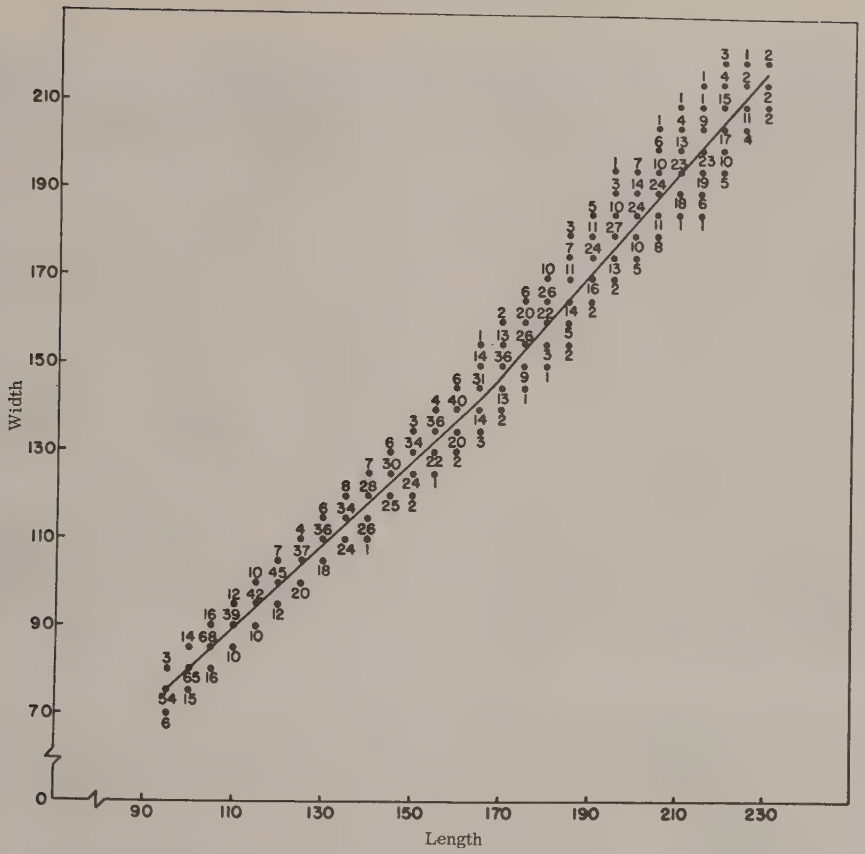


FIG. 41. Length-width relations of larvae of *Tapes semidecussata* during the entire free-swimming veliger stage. Measurements in microns. The figures at dots indicate the numbers of larvae of each dimension.

lighter shell. References in the literature to the larval stages of this form are few. Sullivan (1948) offered a description and photomicrographs of what she assumed were larvae of this bivalve, and Costello *et al.* (1957) discussed the methods of obtaining fertilized eggs and gave a brief description of its early stages of development.

The smallest larvae of *Pitar morrhuana* measure about 70 x 55 μ, although some of them may not be fully formed. Most young straight-hinge larvae measure about 80 x 65 μ (Figs. 42, 43, 44). Upon reaching 125 μ, many larvae display a small umbo which becomes somewhat more prominent as they grow. Setting may begin at 160 μ and is common among larvae measuring about 180 μ. The largest free-swimming larvae were 192 x 179 μ. Even larvae approaching metamorphosis do not have an "eye" spot.

Sullivan (1948) reported that the smallest larvae of *Pitar morrhuana* were 120 x 95 μ, and the largest 220 x 210 μ. Sullivan's smallest larvae thus were about 40 μ larger than ours, and her largest exceeded the maximum size of our larvae by approximately 25 μ. Sullivan, who based her identification on larvae in plankton samples, applied the "indirect method". Later, in personal communication with us, she stated that she had confused the larvae of *Pitar* with those of another species (Loosanoff & Davis, 1950).

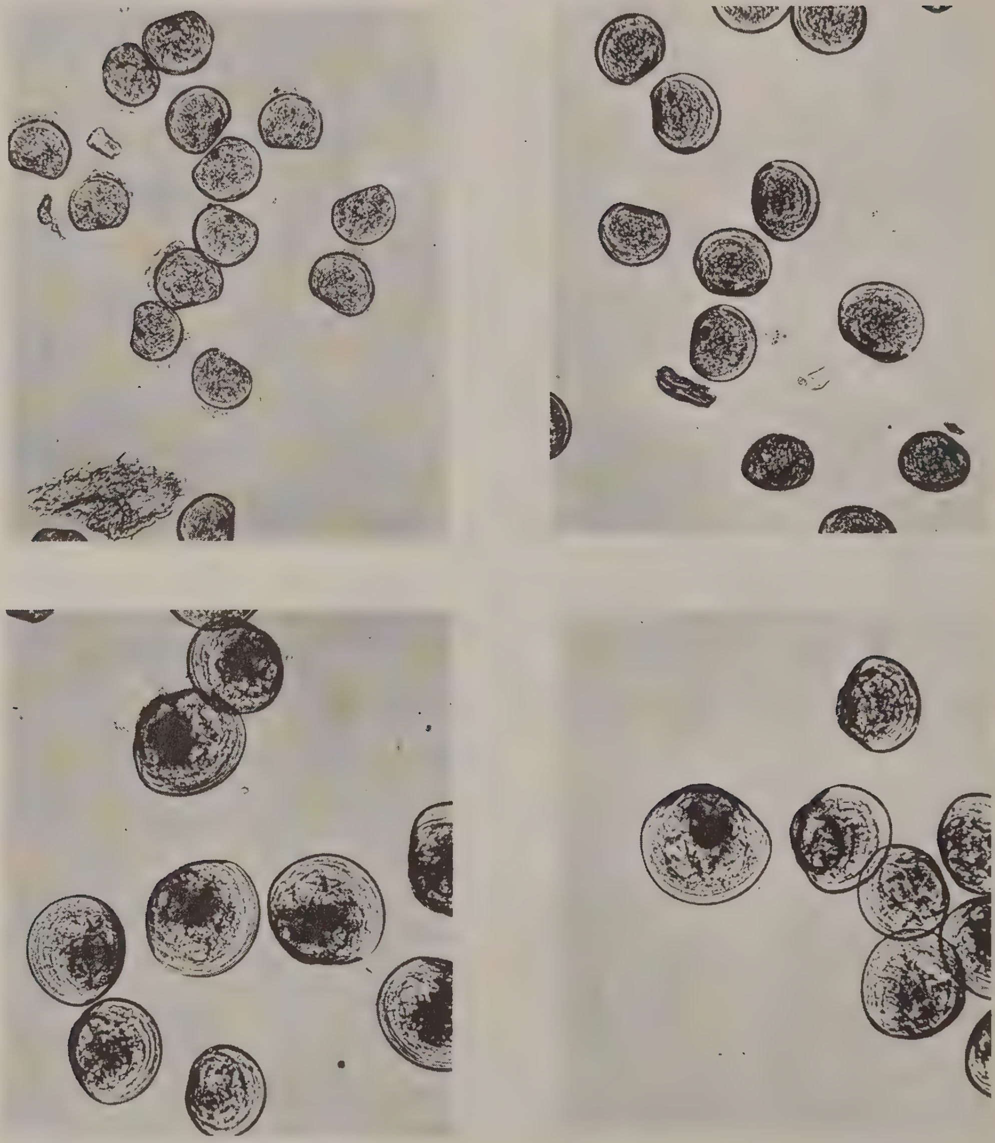


FIG. 42. Group photographs of different sizes of larvae of *Pitar morrhuana*. Smallest individuals of the youngest group are approximately 80 μ long, and the largest of the oldest, approximately 170 μ.

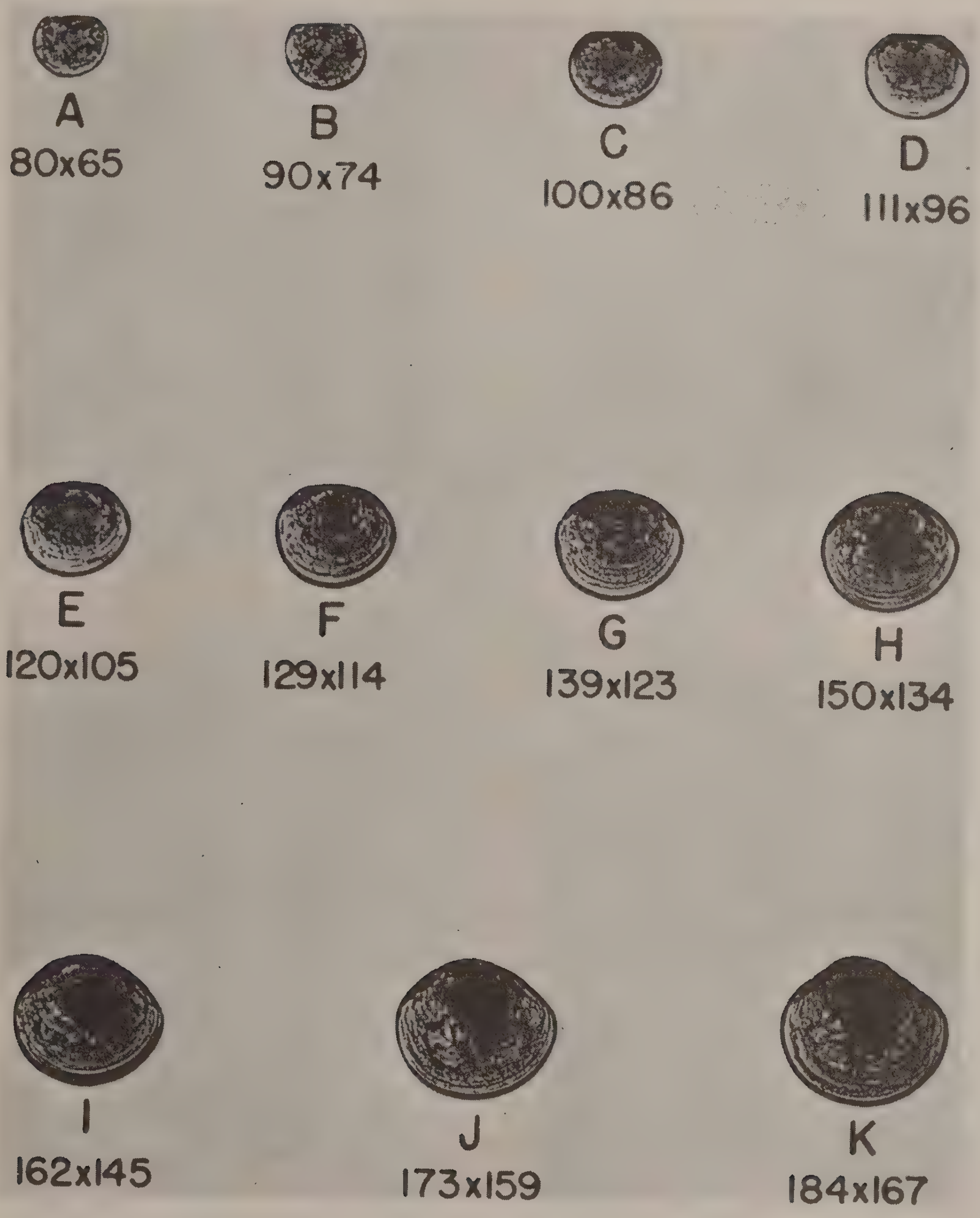

A
80x65
B
90x74
C
100x86
D
111x96
E
120x105
F
129x114
G
139x123
H
150x134
I
162x145
J
173x159
K
184x167

FIG. 43. Photographs of larvae of *Pitar morrhuana* in different stages of development from early straight-hinge stage (A) to the stage of metamorphosis (K). Measurements are in microns; the first figure under a photograph indicates length, and the second, width of the larva.

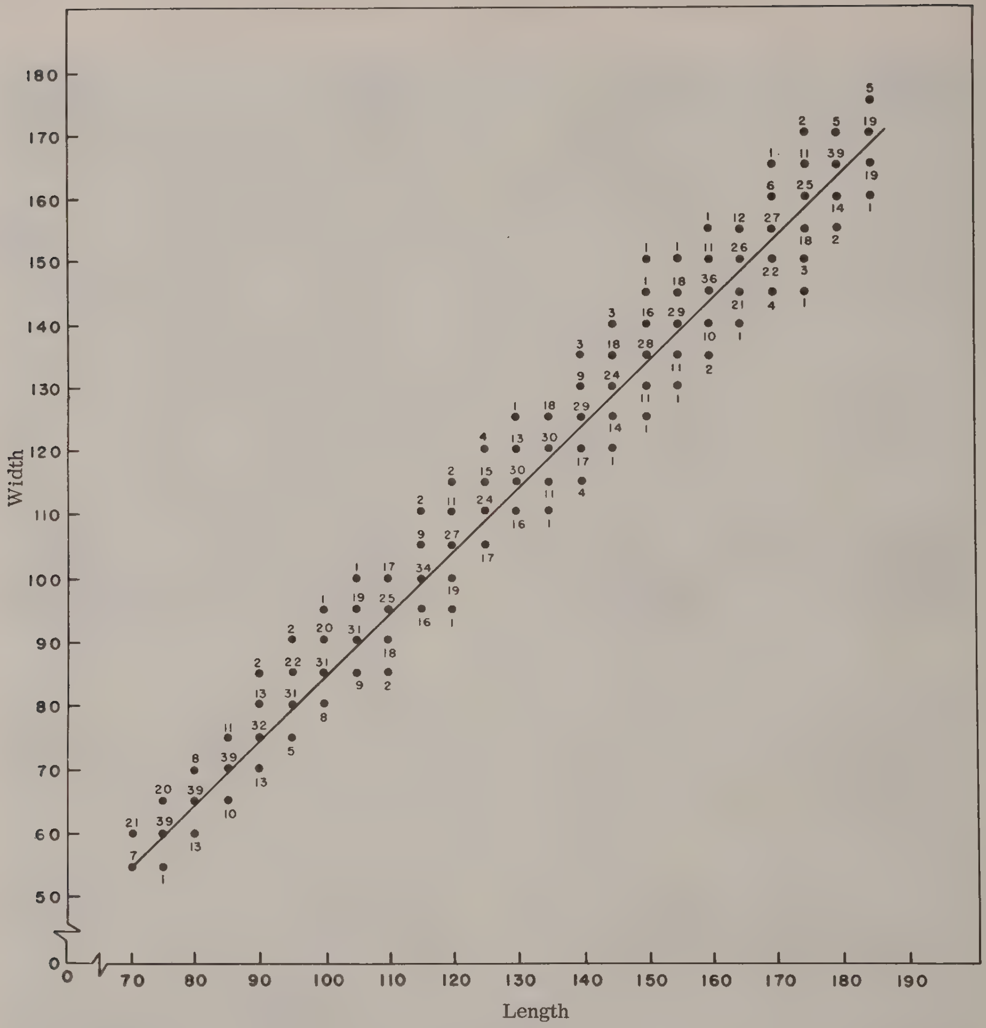


FIG. 44. Length-width relations of larvae of *Pitar morrhuana* during the entire free-swimming veliger stage. Measurements in microns. The figures at dots indicate the numbers of larvae of each dimension.

Again, we call attention to the differences in widths of larvae of the same length (Fig. 44). For example, even during the early stages when the larvae are only 90 μ long, their widths range from 70 to 85 μ. In larger larvae measuring 170 μ long, the widths may vary from 145 to 170 μ, a difference of 25 μ. These variations may be due, in part, to the positions of the larvae on the microscope slides but, nevertheless, the variations are real because even young, relatively flat larvae display them (Fig. 44).

15. *Petricola pholadiformis* Lamarck

This little clam, often called the Rock borer, ranges along our Atlantic coast

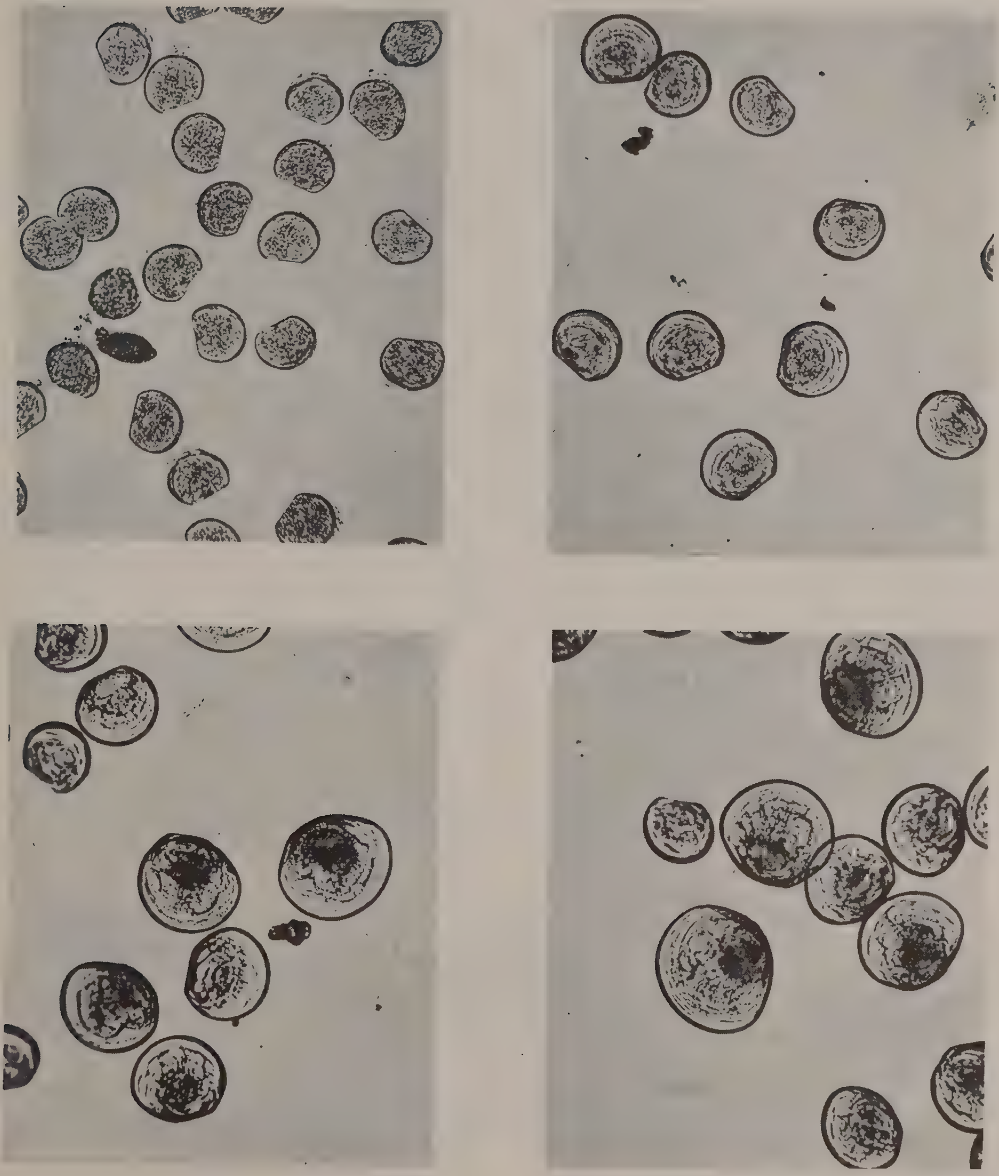


FIG. 45. Group photographs of different sizes of larvae of *Petricola pholadiformis*. Smallest individuals of the youngest group are approximately 80 μ long, and the largest of the oldest, approximately 180 μ.

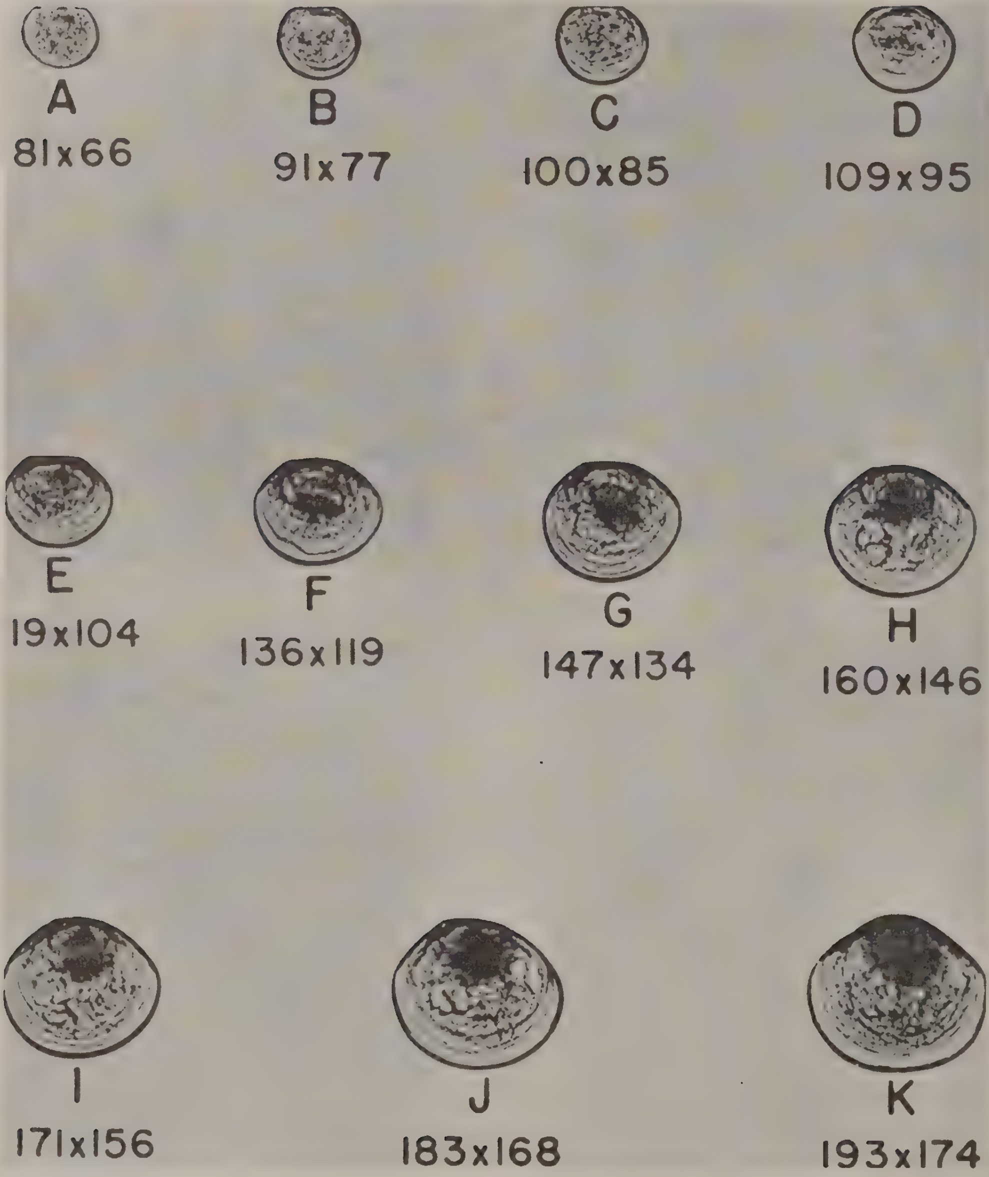

A
81x66
B
91x77
C
100x85
D
109x95
E
19x104
F
136x119
G
147x134
H
160x146
I
171x156
J
183x168
K
193x174

FIG. 46. Photographs of larvae of *Petricola pholadiformis* in different stages of development from early straight-hinge stage (A) to the stage of metamorphosis (K). Measurements are in microns; the first figure under a photograph indicates length, and the second, width of the larva.

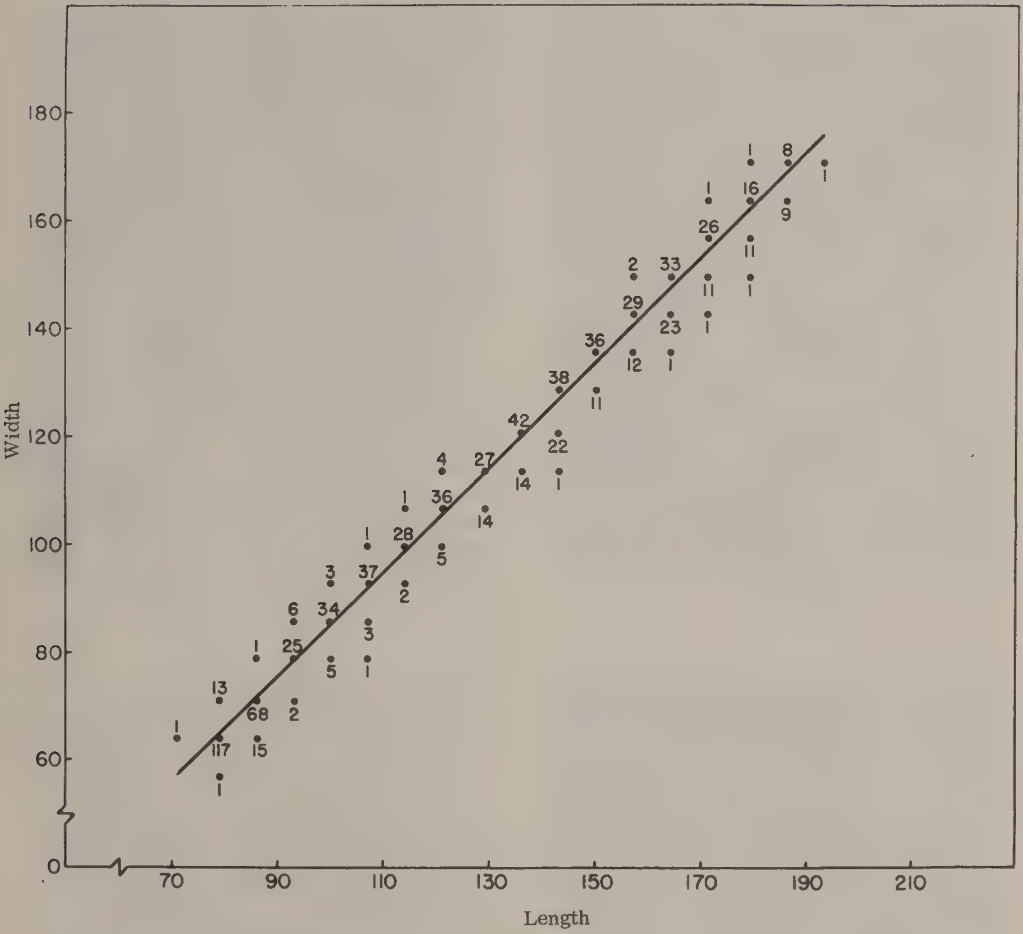


FIG. 47. Length-width relations of larvae of *Petricola pholadiformis* during the entire free-swimming veliger stage. Measurements in microns. The figures at dots indicate the numbers of larvae of each dimension.

from Prince Edward Island south and is also found in the West Indies and some areas of the Gulf of Mexico. Because this species occurs over such a wide range, its larvae should be common in plankton but, strangely enough, Sullivan (1948) and Loosanoff & Davis (1963) are the only authors who offer descriptions. Sullivan said that the larvae of this species appear in plankton in early summer and disappear from the waters of the St. Andrews, New Brunswick, area in early September.

In our laboratory cultures the larvae of *Petricola pholadiformis* measured about 80 x 65 μ at straight-hinge stage (Figs. 45, 46, 47). One or 2 smaller larvae, between 65 and 75 μ long, were seen. In general, our measurements of the straight-hinge larvae are considerably smaller than Sullivan reported. According to her, straight-hinge larvae of this species are relatively large, 115 x 100 μ.

Many larvae begin to metamorphose at a length of about 185 μ, but larvae as large as 193 x 174 μ have been seen swimming in our cultures (Fig. 46). Sullivan's measurements of setting larvae were about 175 x 160 μ, which differs little from the sizes of the smallest metamorphosing larvae in our cultures.

Larvae of *Petricola pholadiformis* are, as a rule, more transparent than those of most other species that we cultured, with the exception of *Anomia simplex* and *Aequipecten irradians*. The early straight-hinge stages are especially transparent and they remain transparent until they metamorphose. According to Sullivan, straight-hinge larvae of this species are pale yellow, whereas older individuals are deep yellow. We do not share this opinion.

16. *Ensis directus* (Conrad)

Ensis directus, the common razor-shell clam of our Atlantic coast, is found in large numbers from Labrador to the Florida Keys. Regardless of its common occurrence, the shelled larvae have been studied only by Sullivan (1948) and Costello *et al.* (1957), who described the early stages of development. Loosanoff & Davis (1963) described the method of cultivation of the species under laboratory conditions.

At early straight-hinge stage the larvae of this clam measure about 92 x 78 μ, although some are occasionally smaller (Figs. 48, 49, 50). They are much more transparent than the larvae of *Mercenaria mercenaria*. The length of the larvae increases more rapidly than the width and at the time of metamorphosis may exceed the width by 40 μ.

The larvae begin to form an umbo when about 115 μ long; this umbo becomes well developed in veligers 130 μ long and longer (Fig. 49). The umbones do not acquire the prominence shown in some other mollusks, for example, the genus *Crassostrea*. The umbo is sufficiently large, however, to prevent larvae from lying flat on the microscope slides. Considerable variation may occur, therefore, in length-width ratios of larvae of the same size.

The smallest metamorphosing larvae in our cultures were only about 210 μ long but some larvae may reach a much larger size before they metamorphose. Several larvae of about 270 μ were still swimming, whereas many already metamorphosed larvae, with a well-developed foot, gills and syphons, measured only about 220 μ.

In most normal larvae of *Ensis directus* 120 μ long or longer a clear area can be easily distinguished around the edge of the shell. This area is noticeable to a length of about 185 μ, but it becomes less pronounced at still greater sizes. This character may be of diagnostic value.

The "eye" spot was not often found even in larger larvae. When it did appear it was not well defined. Sullivan (1948) did not refer to this structure in her studies of the larvae of *Ensis directus*. Werner (1939), working with a related species, stated that its larvae did not have "eye" spots. Jørgensen (1946) mentioned several references to other workers who studied the larvae of closely related forms but found nothing resembling the so-called "eye" spot.

Sullivan (1948) reported that the size range of *Ensis directus* larvae varies from 140 x 120 μ to about 320 x 280 μ. As can be seen from the measurements and photographs (Figs. 48, 49, 50), the sizes of early straight-hinge larvae in our cultures were much smaller than those presented by Sullivan, and our maximum sizes, similarly, were about 50 μ smaller than those observed by her.

Jørgensen (1946) and Rees (1950) gave the dimensions of larvae of several members of the Solenacea of European waters. The measurements of larvae approaching metamorphosis were considerably larger than ours. For example, Jørgensen reported that the largest lar-

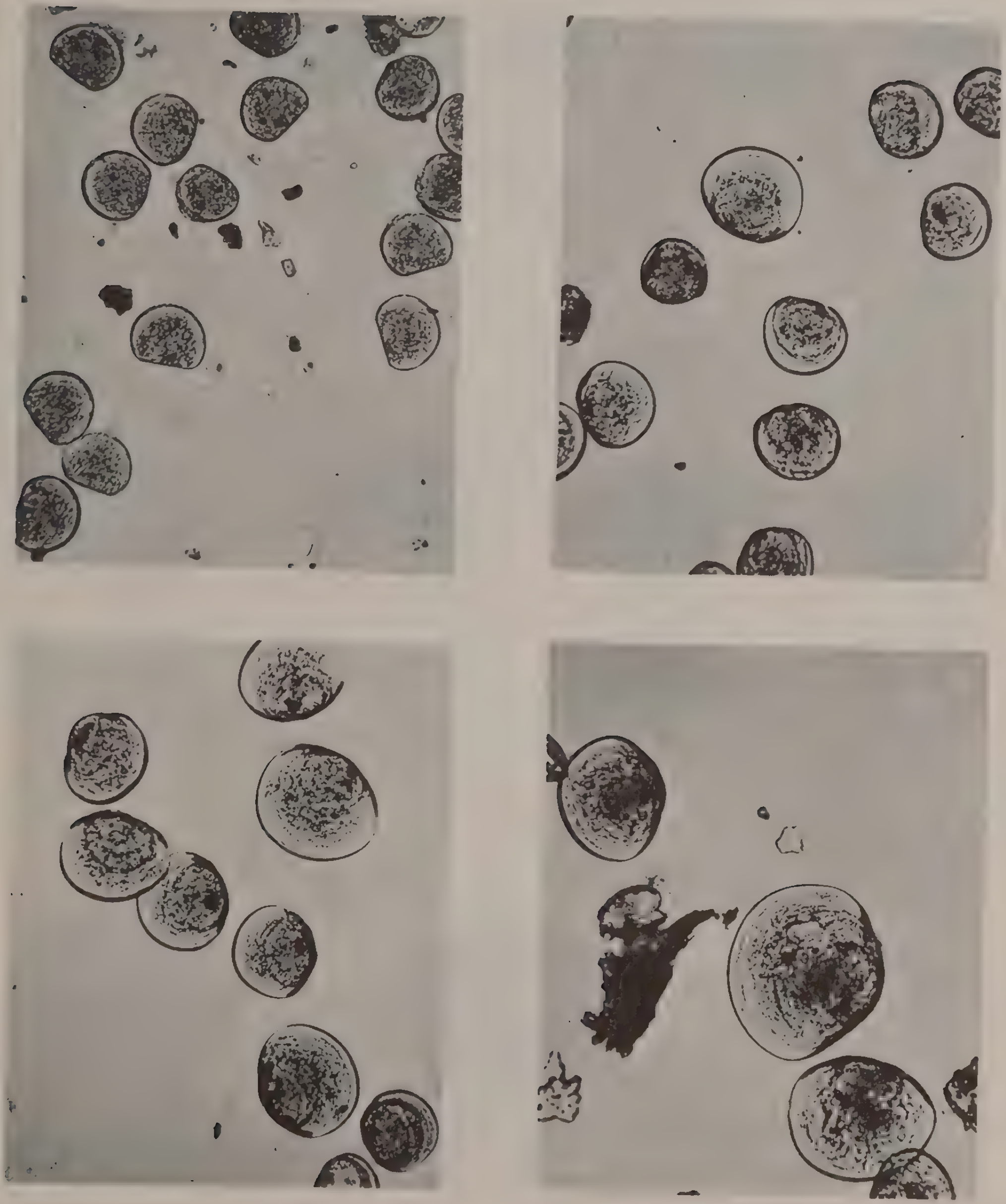


FIG. 48. Group photographs of different sizes of larvae of *Ensis directus*. Smallest normal individuals of the youngest group are approximately 90 μ long, and the largest normal individuals of the oldest approximately 235 μ.

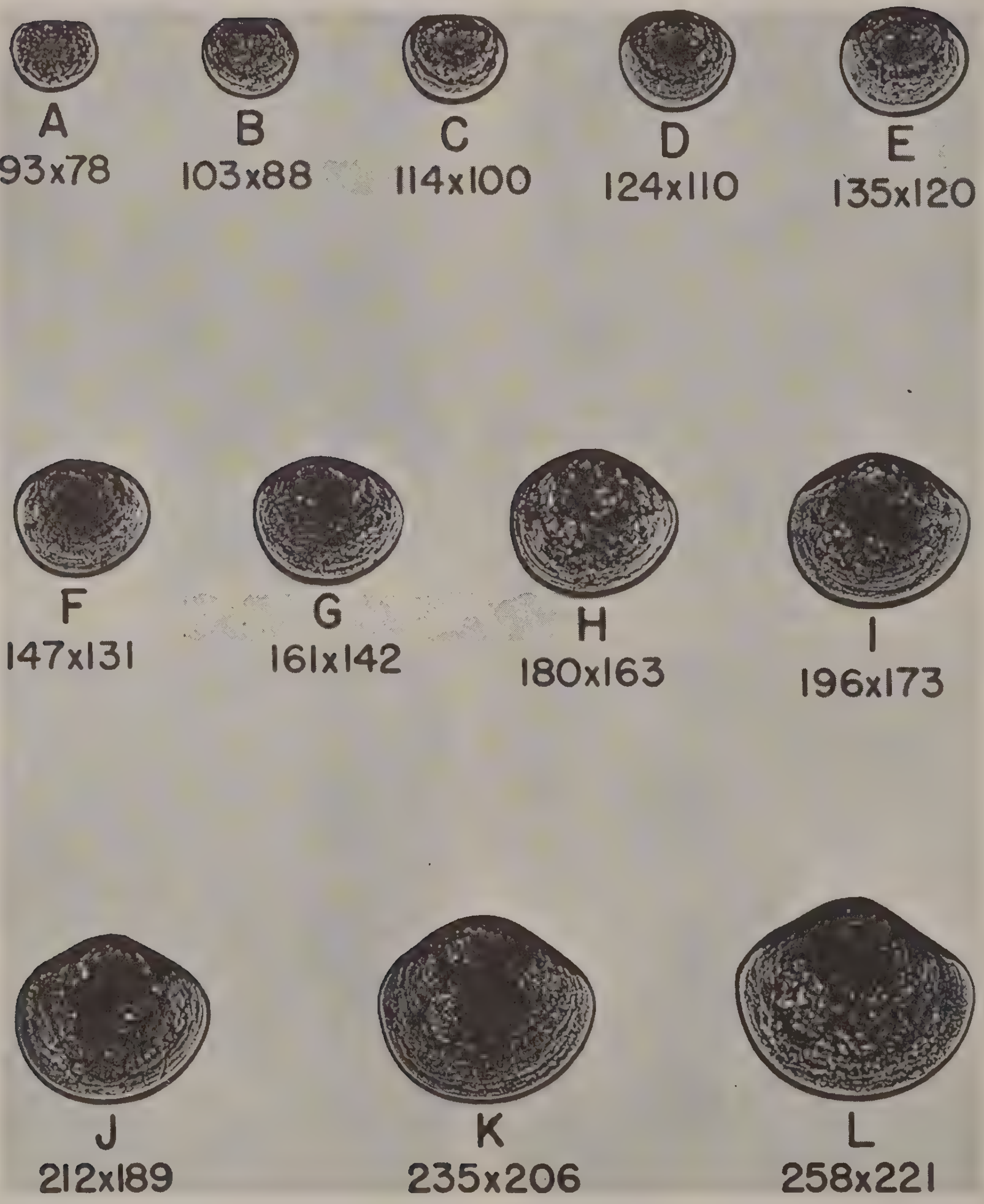

A
93x78
B
103x88
C
114x100
D
124x110
E
135x120
F
147x131
G
161x142
H
180x163
I
196x173
J
212x189
K
235x206
L
258x221

FIG. 49. Photographs of larvae of *Ensis directus* in different stages of development from early straight-hinge stage (A) to the stage of metamorphosis (L). Measurements are in microns; the first figure under a photograph indicates length, and the second, width of the larva.

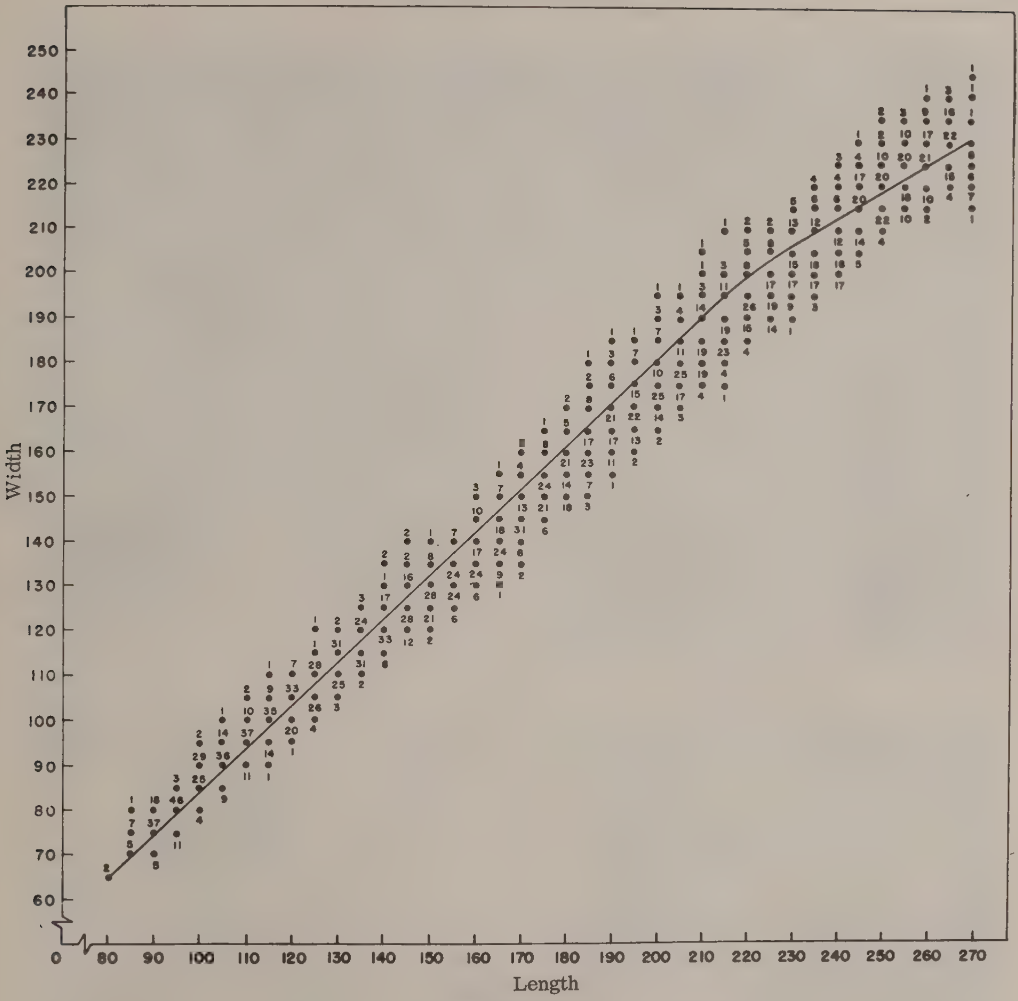


FIG. 50. Length-width relations of larvae of *Ensis directus* during the entire free-swimming veliger stage. Measurements in microns. The figures at dots indicate the numbers of larvae of each dimension.

vae of *Cultellus pellucidus* were up to 360 μ long, and Rees stated that one larva of this species, about 400 μ long, was recorded. The lengths of the larvae given by these 2 authors are larger by about 100 μ than those in our cultures (Figs. 48, 49, 50). Another closely related species, *Ensis siliqua*, mentioned by Lebour (1938) may be about 350 μ long, also much larger than the larvae of our species, *E. directus*. We may add also that the largest larva of *E. directus* shown in the photograph given by Sullivan in her article appears somewhat different from our larvae, and that the 245 μ long larva of *E. ensis* in Rees' photograph has little resemblance to the larvae of *E. directus* of the same size grown at our laboratory (Fig. 49).

17. *Mactra (=Spisula) solidissima* Dillwyn

This mollusk, commonly called the

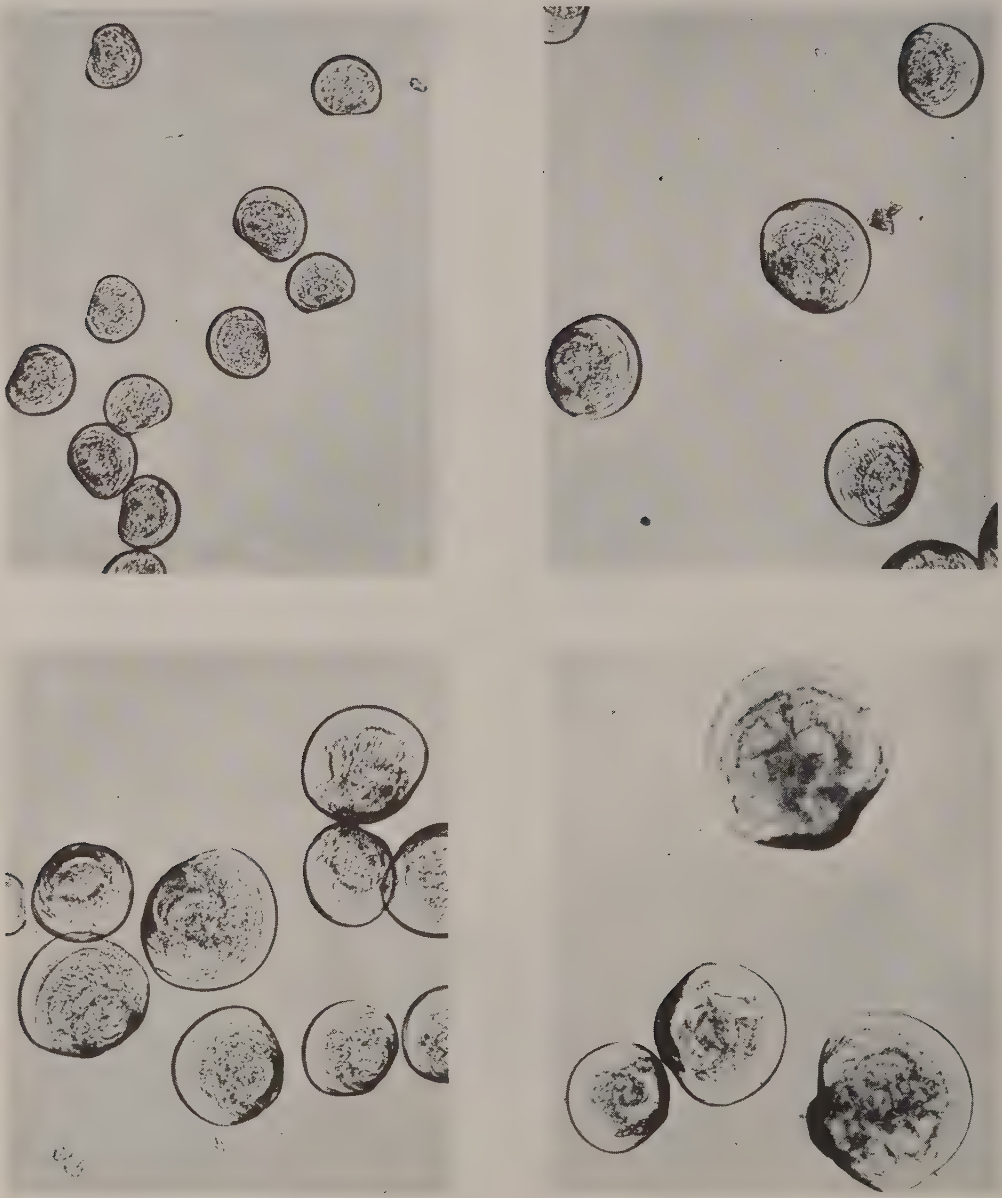


FIG. 51. Group photographs of different sizes of larvae of *Mactra solidissima*. Smallest individuals of the youngest group are approximately 72 μ long, and the largest of the oldest, approximately 218 μ.

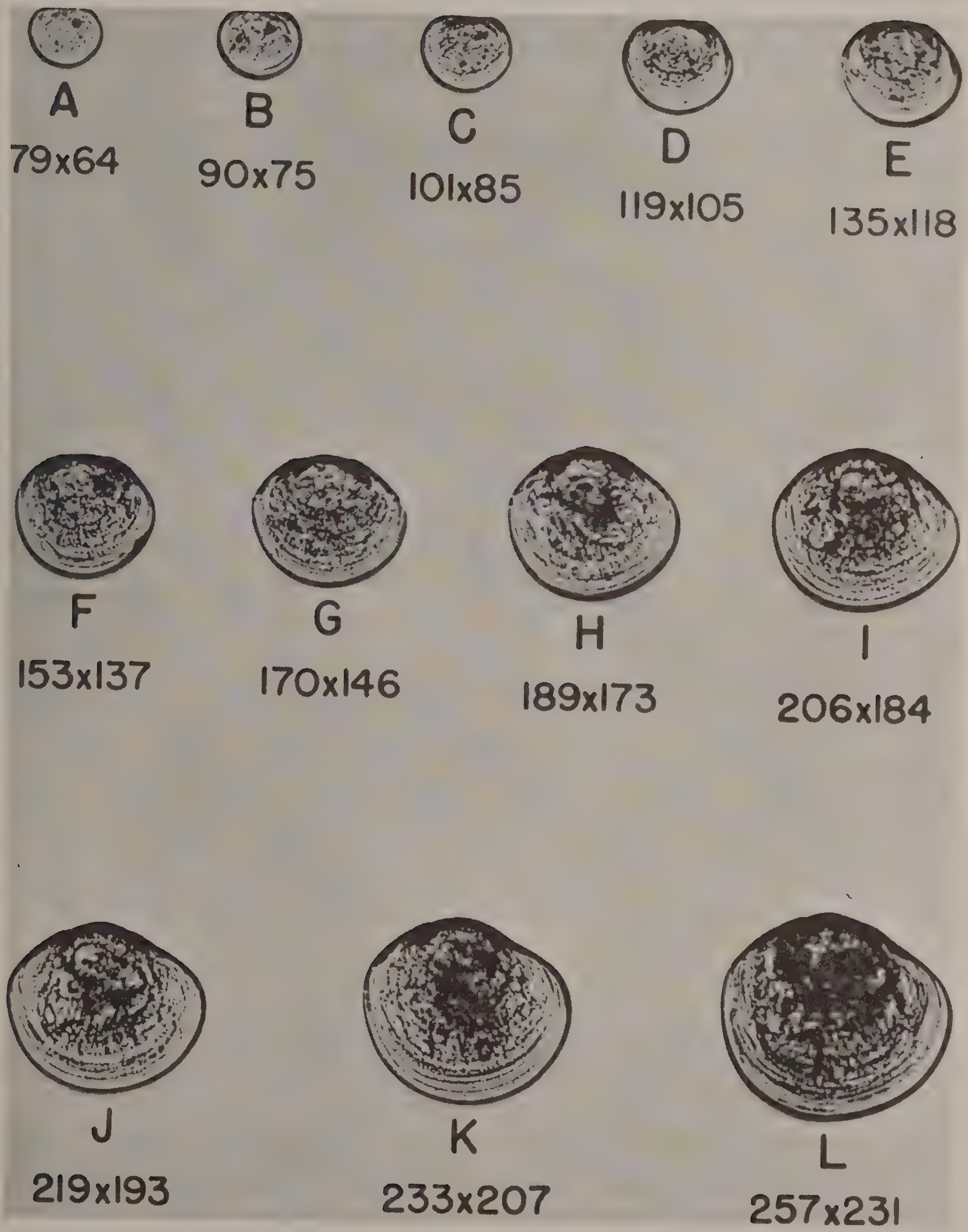

A
79x64
B
90x75
C
101x85
D
119x105
E
135x118
F
153x137
G
170x146
H
189x173
I
206x184
J
219x193
K
233x207
L
257x231

FIG. 52. Photographs of larvae of *Mactra solidissima* in different stages of development from early straight-hinge stage (A) to the stage of metamorphosis (L). Measurements are in microns; the first figure under a photograph indicates length, and the second, width of the larva.

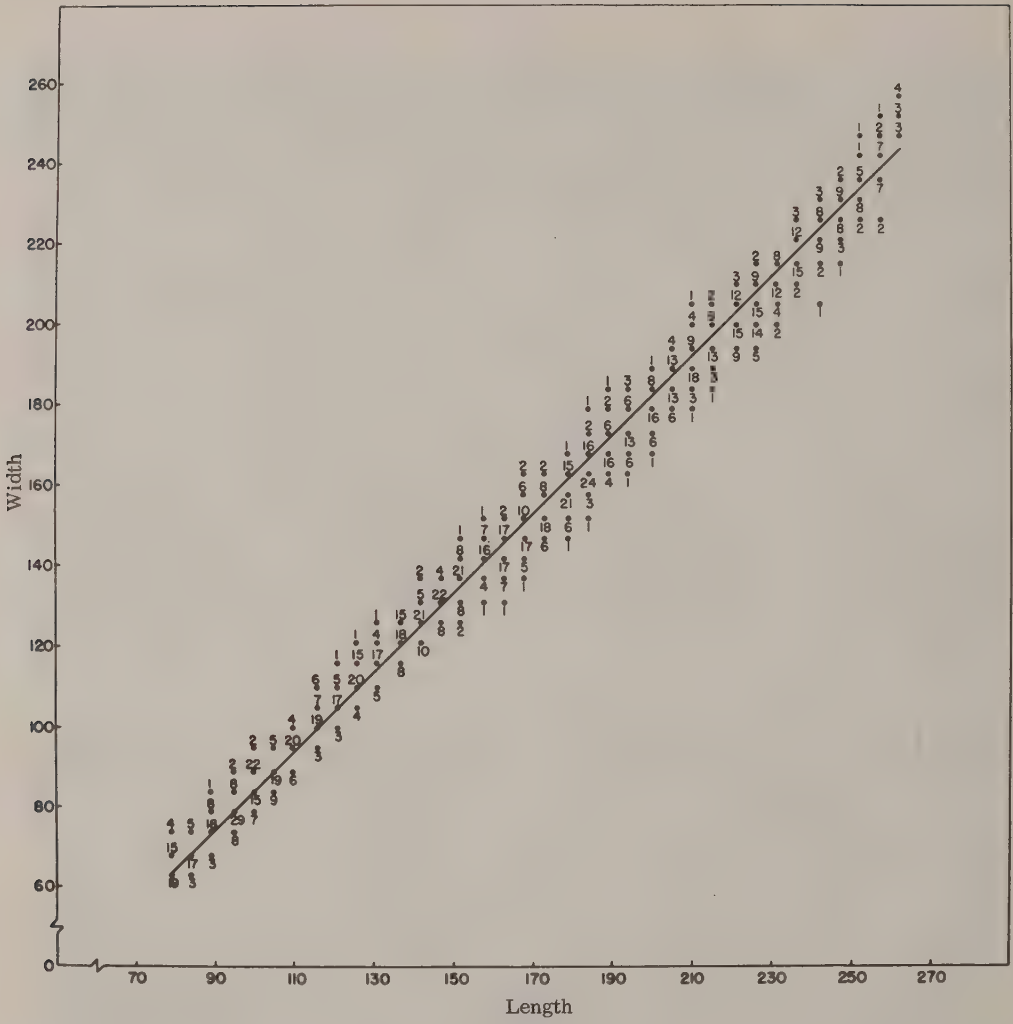


FIG. 53. Length-width relations of larvae of *Mactra solidissima* during the entire free-swimming veliger stage. Measurements in microns. The figures at dots indicate the numbers of larvae of each dimension.

Surf clam, is the largest bivalve of our Atlantic coast, sometimes measuring almost 7-1/2 inches in length. It is extremely abundant in some sections of its range, which extends from Labrador to Cape Hatteras.

The early normal straight-hinge larvae of this clam are approximately 80 x 65 μ (Figs. 51, 52, 53). Our cultures sometimes contained smaller larvae, but they usually showed some anatomical abnormality. As with several other species, the larvae of *Mactra solidissima* display considerable differences and variations in the sizes at which certain organs begin to be discernible or at which they begin to metamorphose. Some larvae may have a well-formed foot when they are only 160-165 μ long although, as a rule, this organ appears when the larvae are near 215 μ long. When the length is about 240 μ, most larvae display a strong, functional foot.

A few individuals are fully metamorphosed when only about 220 μ long. Normally, however, a larva is between 230 and 250 μ long before it settles. Occasionally larvae measuring slightly over 260 μ long were still swimming in our cultures.

In general, our studies on the development and growth of larvae of *Mactra solidissima* closely agree with those of Imai *et al.* (1953b), who studied the development of a related species, *M. sachalinensis*. Both Imai's group and ours worked with larvae of known parents grown under controlled laboratory conditions. Sullivan (1948) gave the size range for larvae of *M. solidissima* from 95 x 80 μ to 270 x 245 μ. Thus, her smallest larvae were about 15 μ longer than ours; the maximum size was similar to ours.

Jørgensen (1946), describing *Spisula subtruncata*, a European form closely related to our clam, reported that metamorphsis in that species took place at the length of about 400 μ or more. This size is considerably larger than we observed among the larvae in our cultures and is also larger than the measurements goven by Kändler (1926), who recorded the length of metamorphosing larvae of *S. subtruncata* as only 310 μ. Rees' (1950) measurements of larvae, which he considered as belonging to the family Mactracea, were also considerably larger than ours. Rees gave the length of advanced stages of larvae, presumably those of *Spisula solida*, as 360 μ and of *S. elliptica* as 355 μ. These measurements exceed by almost 100 μ the maximum length of the larvae of *Mactra solidissima* reared in our experiments and the larvae of *M. sachalinensis* grown by Imai *et al.* (1953b). The photomicrographs of *S. solida* offered by Rees in his article bear little resemblance to our larvae of *M. solidissima* because of the strongly pronounced concentric lines of the shell of the European species. His picture is obviously of a juvenile, not a larva. Moreover, the general shapes of older larvae of *S. subtruncata* offered in his photomicrographs do not closely resemble the outlines of the advanced stages of larvae of *M. solidissima* (Fig. 52). Moreover, the remarks by Rees in the discussion of the superfamily Mactracea indicate much uncertainty about the appearance and sizes of larvae of this group. Rees himself pointed out the wider disagreement about specific boundaries in this group than in any other. We agree on this point because of the differences in sizes of metamorphosing larvae studied by Imai *et al.* (1953b) and ourselves and of those described by Rees.

Some of Rees' statements are almost incompatible with our findings. For example, in his discussion of what he called "Mactrid E", characterized by *Mactra corallina*, Rees (1950) stated that the mactrid tooth, which is, presumably, characteristic of this entire group, is not formed even in larvae as large as 290 μ but appears later. None of our larvae nor those of Imai, Kändler or Sullivan measured 290 μ at the time of metamorphosis, a size that according to Rees was still characteristic of immature larvae without mactrid teeth.

18. *Mya arenaria* Linnaeus

This extremely common clam of our Atlantic coast ranges from the Canadian border to North Carolina. It has also been introduced with shipments of eastern oysters to the Pacific coast where it is now comparatively abundant.

Again, as with other pelecypods, it is difficult to indicate the smallest normal size of straight-hinge larvae. In our cultures straight-hinge larvae measuring only about 86 μ long were seen occasionally. Most fully formed larvae, however, were about 90 x 75 μ (Figs. 54, 55, 56). Throughout the entire growth the length of the larval shell

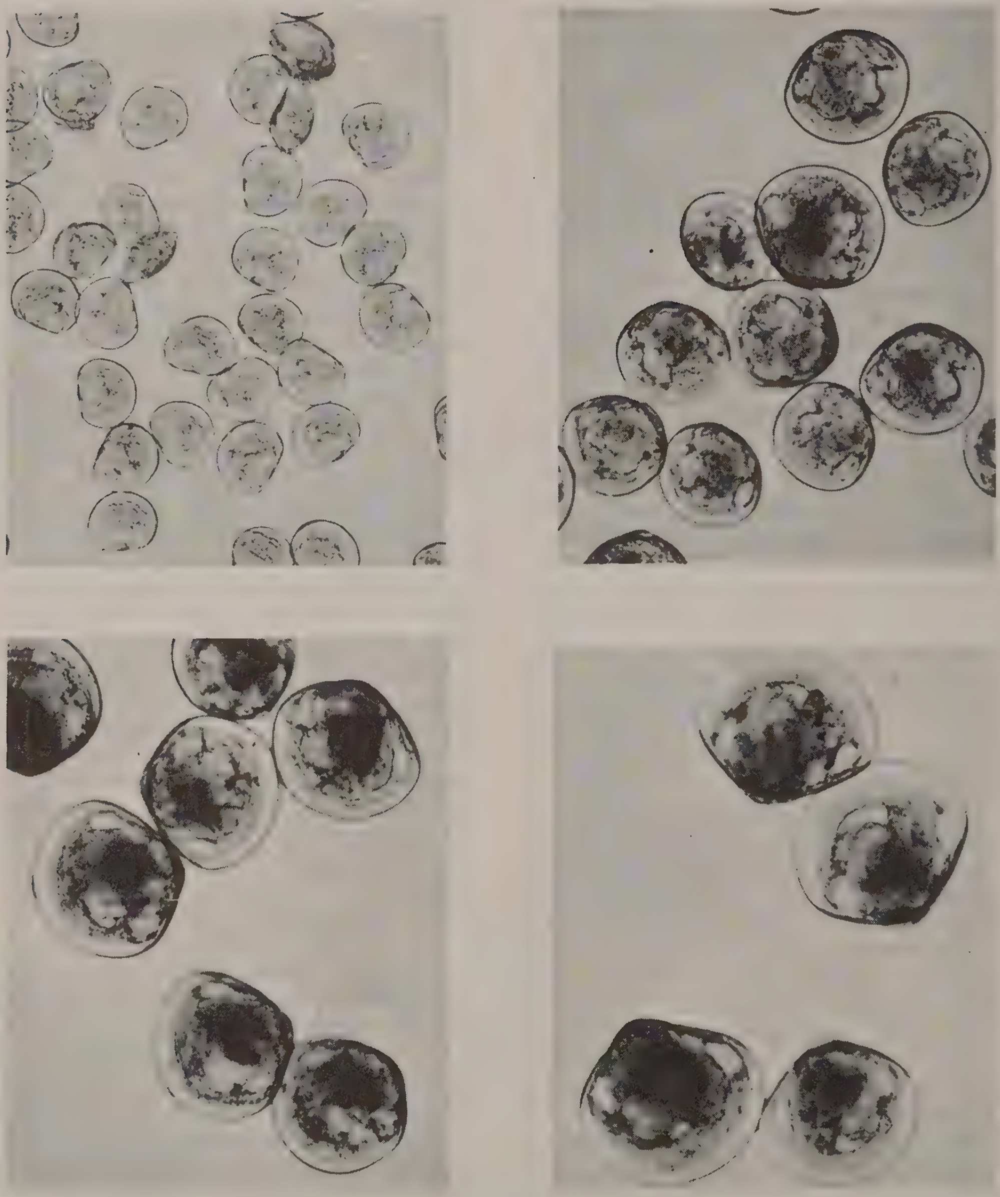


FIG. 54. Group photographs of different sizes of larvae of *Mya arenaria*. Smallest individuals of the youngest group are nearly 93 μ long, and the largest of the oldest group are approximately 230 μ; some of them are near, or in the process of metamorphosis.

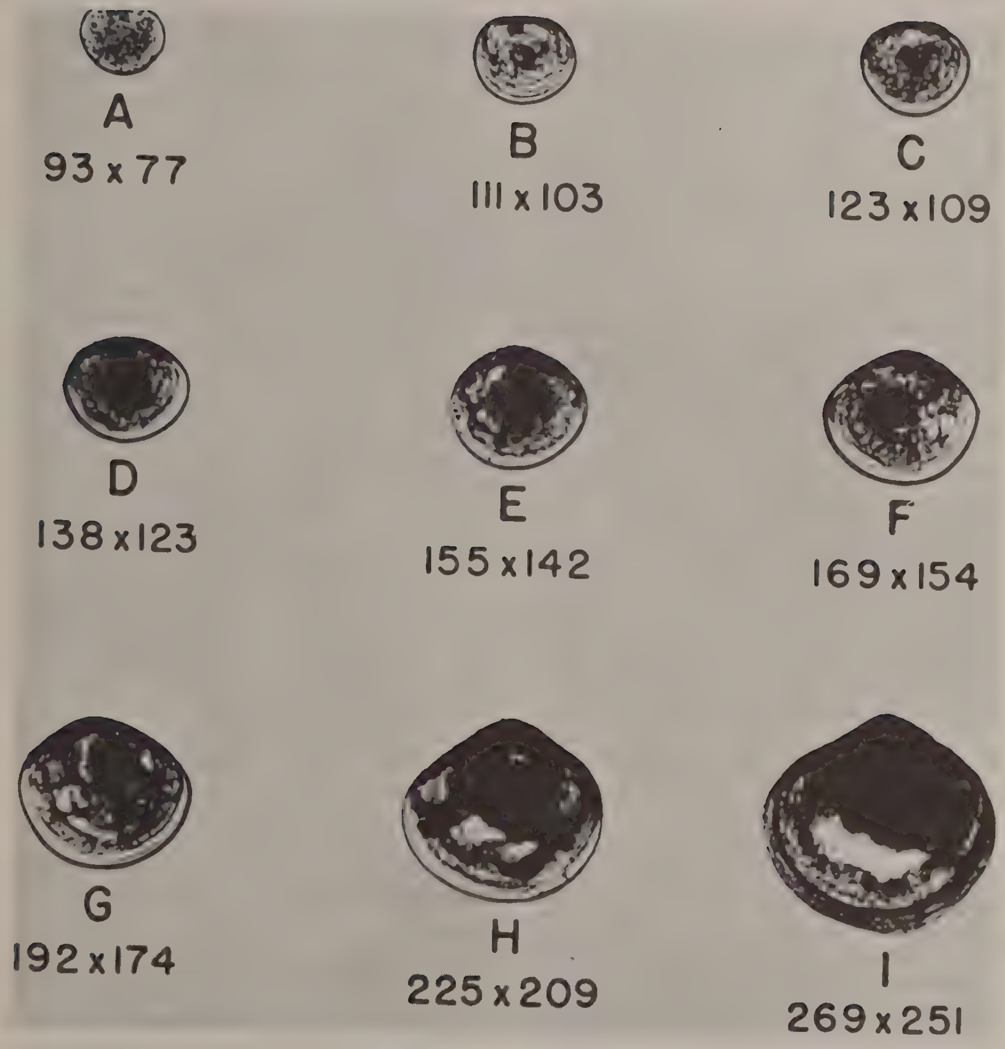

A
93 x 77
B
111 x 103
C
123 x 109
D
138 x 123
E
155 x 142
F
169 x 154
G
192 x 174
H
225 x 209
I
269 x 251

FIG. 55. Photographs of larvae of *Mya arenaria* in different stages of development from early straight-hinge stage (A) to the stage of metamorphosis (H). The last figure (I) is that of a recently metamorphosed individual. Measurements are in microns; the first figure under a photograph indicates length, and the second, width of the larva.

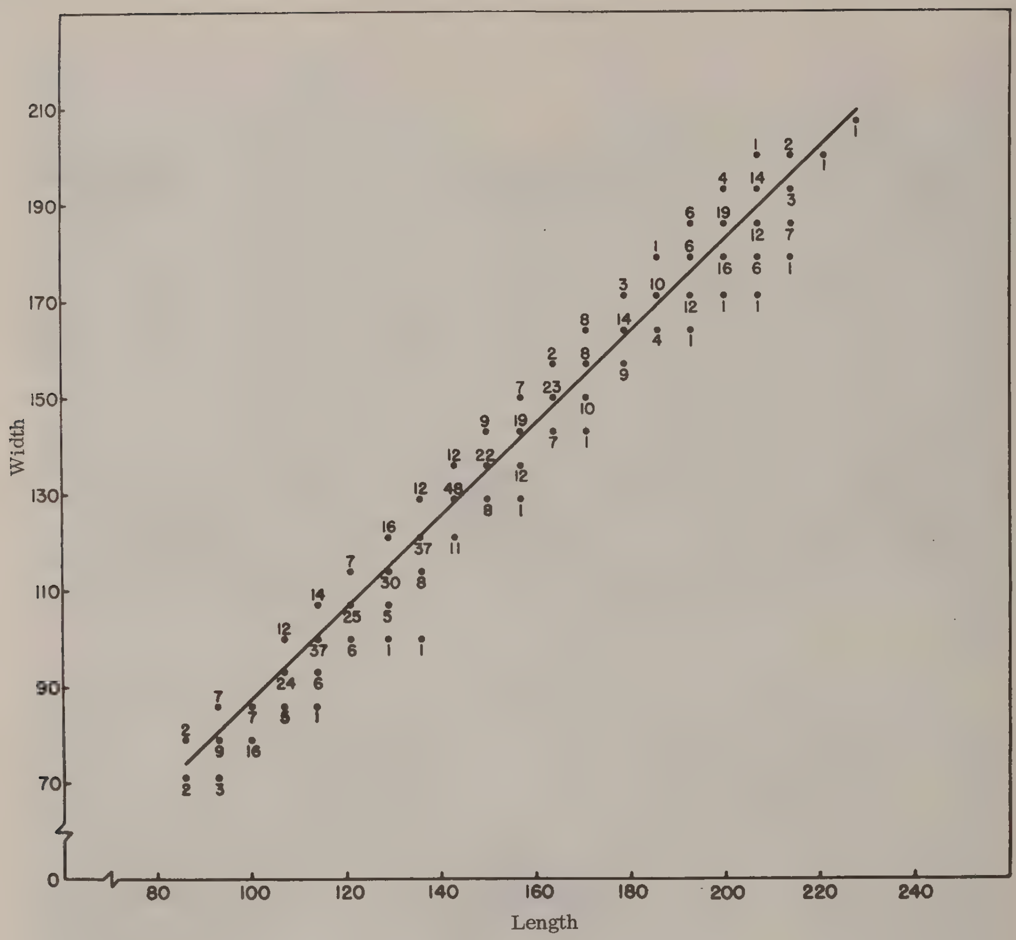


FIG. 56. Length-width relations of larvae of *Mya arenaria* during the entire free-swimming veliger stage. Measurements in microns. The figures at dots indicate the numbers of larvae of each dimension.

remains greater than its width.

The larvae of *Mya arenaria* are light-colored, especially during early development (Fig. 54). When the larvae reach 110 μ their shells become somewhat darker. Larvae 175 μ or longer have irregular opaque spots, measuring 5-15 μ in diameter and located along the margin of the shells. Since these spots occur regularly, they may be characteristic of this species, especially of the late larval stages. Jørgensen (1946) also noticed the pigmented areas of the soft parts of larvae of *M. arenaria* over 200 μ long and believed that these spots may be a reliable character for identification.

The size range within which metamorphosis of the larvae of *Mya arenaria* occurred in our experimental cultures extended from about 170-230 μ; however, the majority of the larvae began to metamorphose soon after they reached 200 μ. Almost the same observations were made by Stickney (1964), who studied the larvae of *M. arenaria* that came from widely separated areas of the Atlantic coast.

The smallest larva with a well-developed foot was about 165 μ long. The velum normally began to disappear after the length of 175 μ was reached, and, as a rule, the velum was already completely or almost completely resorbed in most individuals that measured over 200 μ. In some cultures, individuals only 175 μ long were crawling on the bottom of culture vessels and using their foot energetically. The otocyst could be seen in larvae approximately 175 μ long, and the byssus gland was easily discerned at approximately 200 μ.

Larvae assumed to be those of *Mya arenaria* have been described by several investigators. Stafford (1912) reported that the largest such larva he measured was 414 x 345 μ. These measurements are almost twice as large as those we made on metamorphosing individuals in our cultures. We suspect, therefore, that Stafford measured either the larva of a species other than *M. arenaria* or an individual that had metamorphosed some time earlier. Since, however, his measurements were consistently larger than ours for all species, it is possible that he erred in his measurements. Sullivan (1948) gave the size range of larvae of *M. arenaria* as extending from 105 x 90 μ to 250 x 230 μ. These figures, in general ral, are close to ours. Jørgensen (1946) reported that the size of metamorphosing larvae of *M. arenaria* is extremely variable, ranging from about 200-300 μ. Even though the maximum size of larvae given by Jørgensen is much larger than ours, we agree with him that the difference in sizes of larvae of *M. arenaria* at setting is considerable. In studies of a closely related species, *Mya truncata*, Jørgensen concluded that the maximum size of its larvae is about 320 μ, considerably larger than the maximum size of the larvae of *M. arenaria* grown under controlled conditions (Loosanoff & Davis, 1963; Stickney, 1964). Yoshida (1938) found that the size at which larvae of *Mya japonica* metamorphosed varied from 240 x 220 μ to 300 x 260 μ. The maximum sizes of the metamorphosing larvae offered by Yoshida, therefore, are approximately 70 μ larger than ours.

19. *Teredo navalis* Linnaeus

Teredo navalis, often called the common shipworm, is found along both coasts of the United States and also in Europe and Asia. It is a larviparous bivalve, releasing its larvae when they are already veligers in the straight-hinge stage.

In our laboratory the smallest larvae released measured 80 x 70 μ, whereas the largest larvae recently discharged or found in the mantle chamber of the mother mollusk were 90 μ long. This size is about 10 μ larger than was reported by Jørgensen (1946). In general, however, our observations on the size of recently released larvae of *Teredo navalis* (Figs. 57, 58, 59) are in agreement with those of Imai *et al.* (1950a), Sullivan (1948) and Jørgensen (1946). We disagree, though, with the observations of Lane *et al.* (1954), who stated that the larvae of *T. navalis* are about 250 μ long at the time they are released from the gill chamber of the mother.

The shells of even recently released larvae are heavy and thick, and are characterized by a dark band around the edge (Figs. 57, 58). Sometimes another light band may be seen clearly inside of the darker outside band. This band remains distinguishable until metamorphosis. As the larvae grow, the color of their shells gradually becomes darker.

Several fully metamorphosed young *Teredo* measuring only 190 μ in length were found on the bottom of our culture vessels. The largest swimming larvae in our cultures were only slightly longer than 200 μ (Figs. 58, 59). These measurements are similar to those of Sullivan (1948) and Imai *et al.* (1950a), although their maximum measurements exceed ours by about 10 μ.

The larvae of *Teredo* do not develop

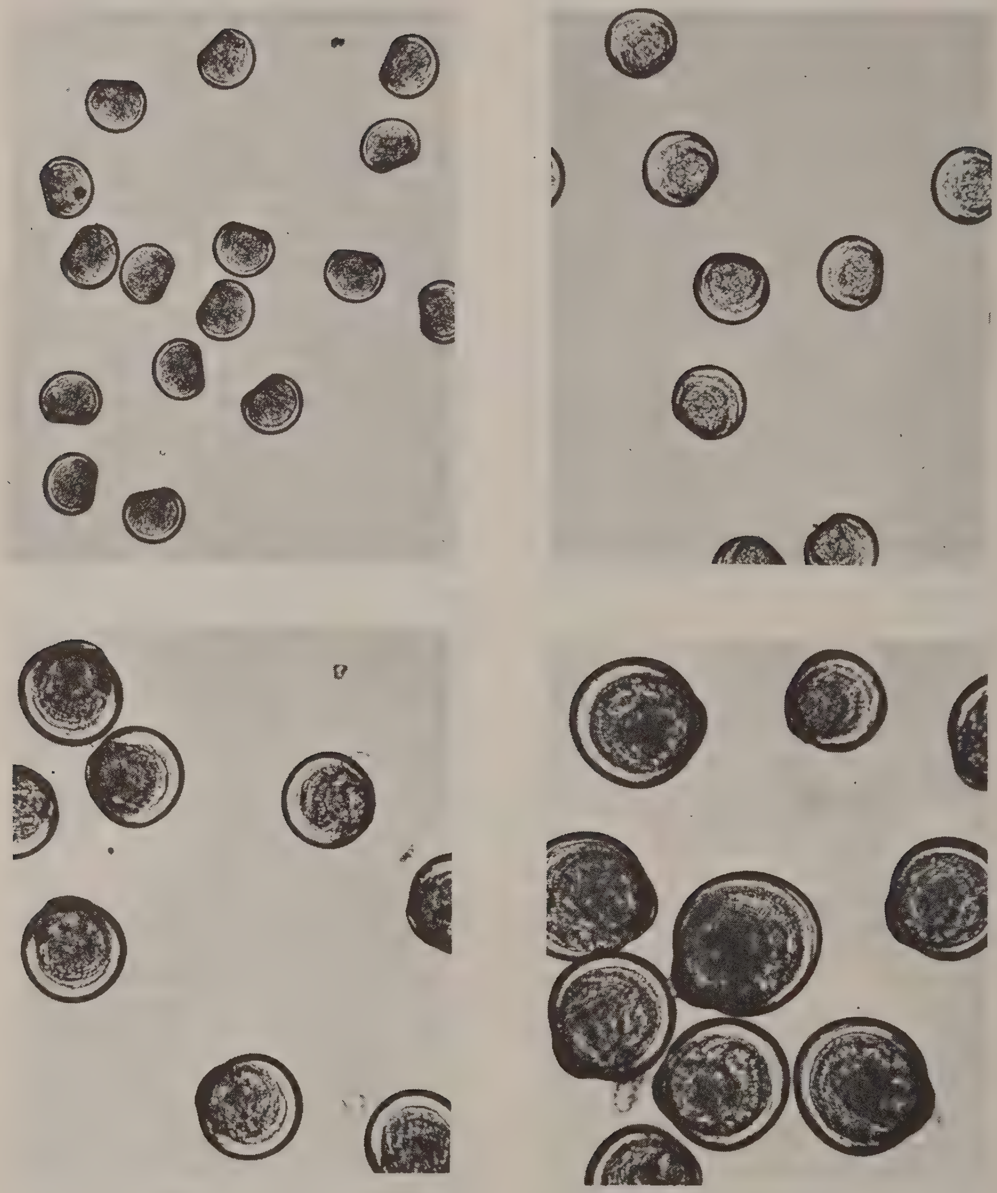
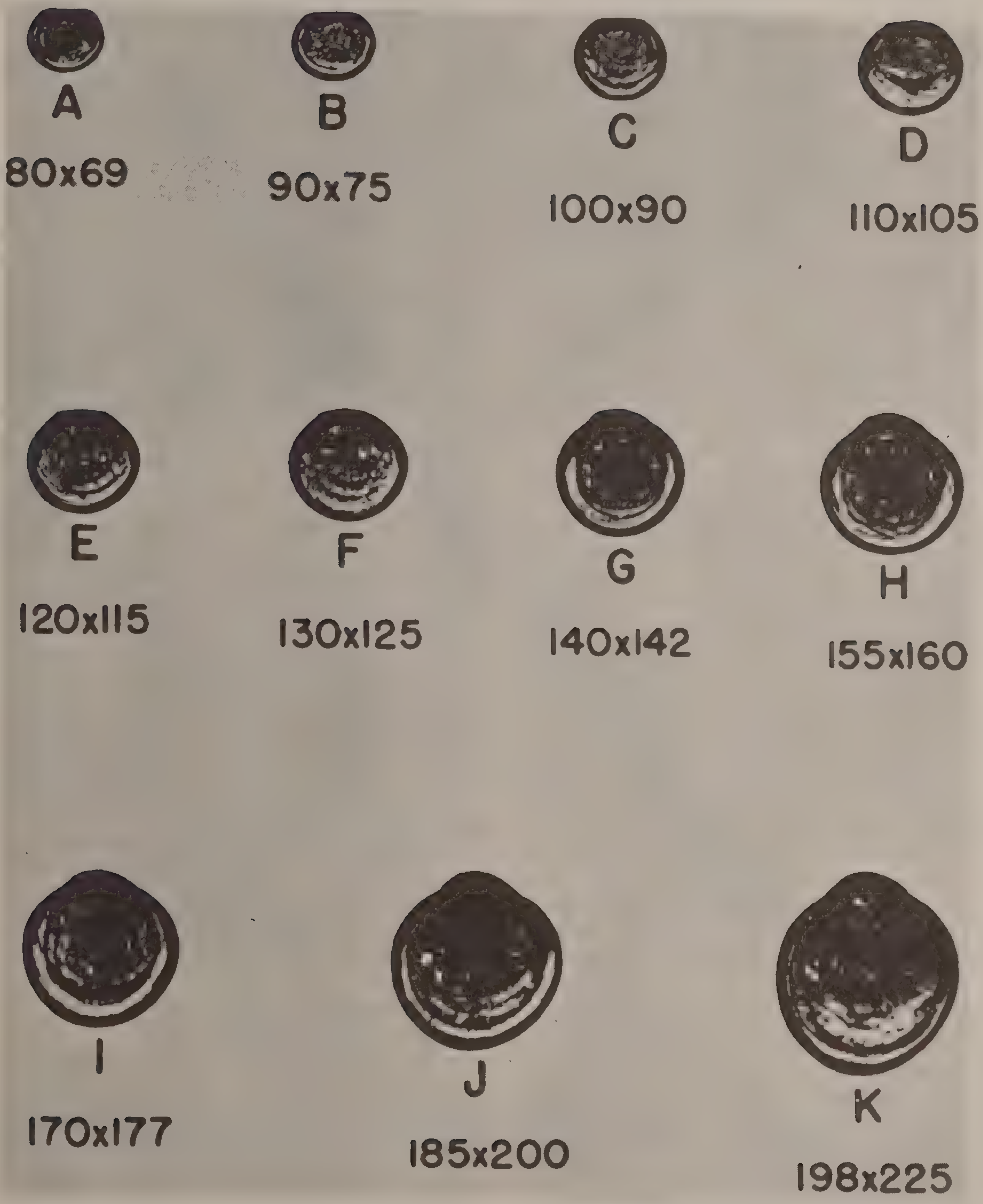


FIG. 57. Group photographs of different sizes of larvae of *Teredo navalis*. Smallest individuals of the youngest group are approximately 80 μ long, and the largest of the oldest, approximately 185 μ.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B
90x75
C
100x90
D
110x105
E
120x115
F
130x125
G
140x142
H
155x160
I
170x177
J
185x200
K
198x225

FIG. 58. Photographs of larvae of *Teredo navalis* from the time they are released in swarming by the parents (A) until the time of metamorphosis (K). Measurements are in microns; the first figure under a photograph indicates length, and the second, width of a larva.

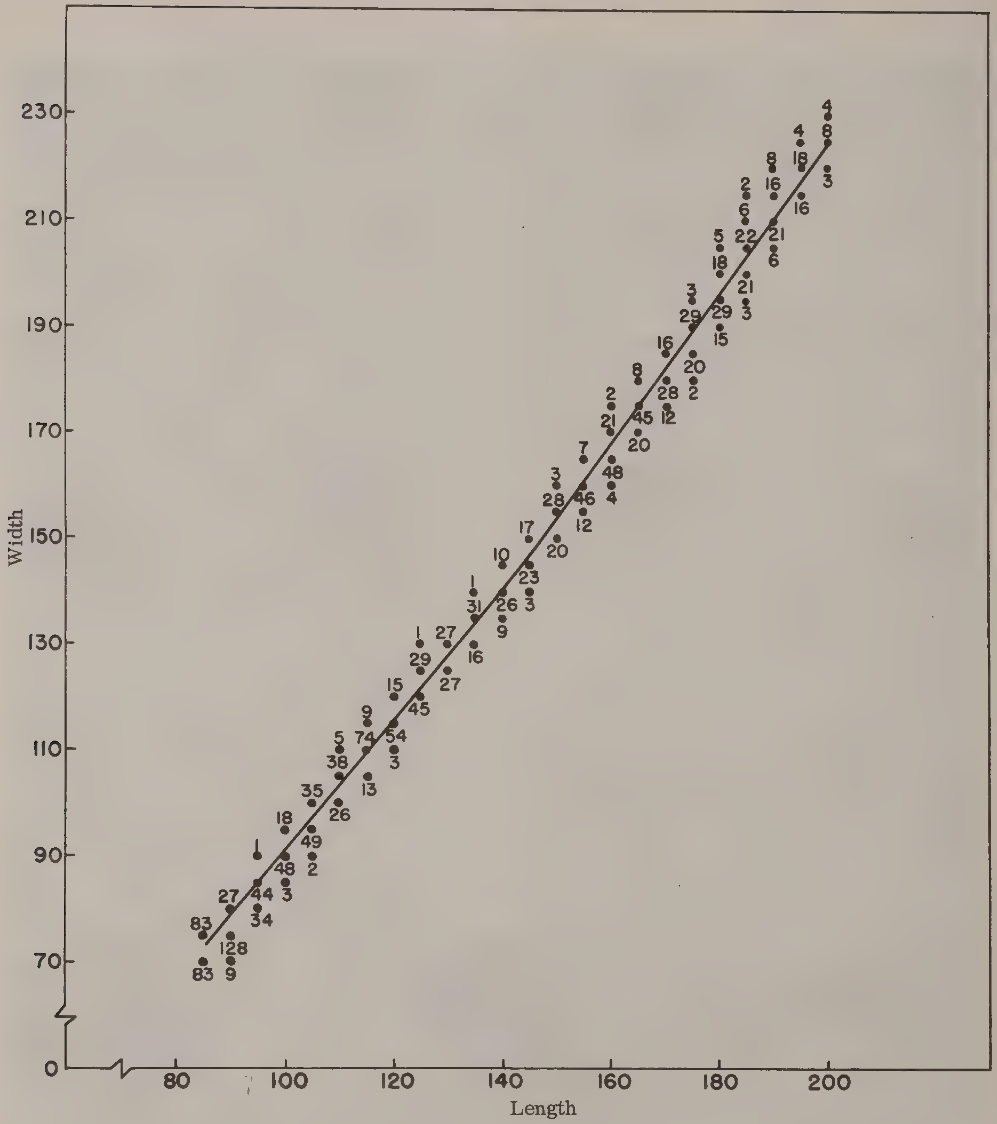


FIG. 59. Length-width relations of larvae of *Teredo navalis* during the entire free-swimming veliger stage. Measurements in microns. The figures at dots indicate the numbers of larvae of each dimension.

the "eye" spot that is found in mature larvae of some other species of bivalves. Details on the rearing of *Teredo* larvae under laboratory conditions and information about their behavior are given in the recent article of Loosanoff & Davis (1963).

Jørgensen (1946) offered information on the larvae of a closely related species of European waters, *Teredo nor-*

vegica. According to him the oldest veligers of this species may be approximately 300 μ long and are almost circular; thus their shape differs from that of the larvae of *T. navalis* (Fig. 58). Furthermore, some veligers of *T. norvegica* possessed a black "eye" spot, a structure not found in *T. navalis*. The larvae of yet another species, *T. megotara*, described by Jørgensen, contained individual veligers up to about 330 μ long.

20. *Laevicardium mortoni* (Conrad)

This small bivalve, which is very abundant from Martha's Vineyard, Massachusetts, to New Jersey, U. S. A., is found from Nova Scotia to Brazil. It is known by several common names, including Morton's cockle. As far as we could determine, no description of the larvae of this species is found in the literature.

The smallest straight-hinge larva of this cockle in our laboratory cultures measured approximately 85 x 70 μ. Most larvae at this stage, however, were a few microns larger (Figs. 60, 61). Length of the larval shell increases more rapidly than its width, and at metamorphosis the length may exceed the width by more than 30 μ. The margin of the straight-hinge larval shell is outlined by a dark band resembling the band in *Teredo* larvae, but not so prominent. At almost all stages, especially near metamorphosis, one end of the larval shell is longer and somewhat more pointed than the other (Fig. 60). Soon after a length of about 135 μ is reached the umbo begins to appear; it becomes prominent when the shell length is about 160 μ. No "eye" spot was observed in the larvae, even in those reaching metamorphosis.

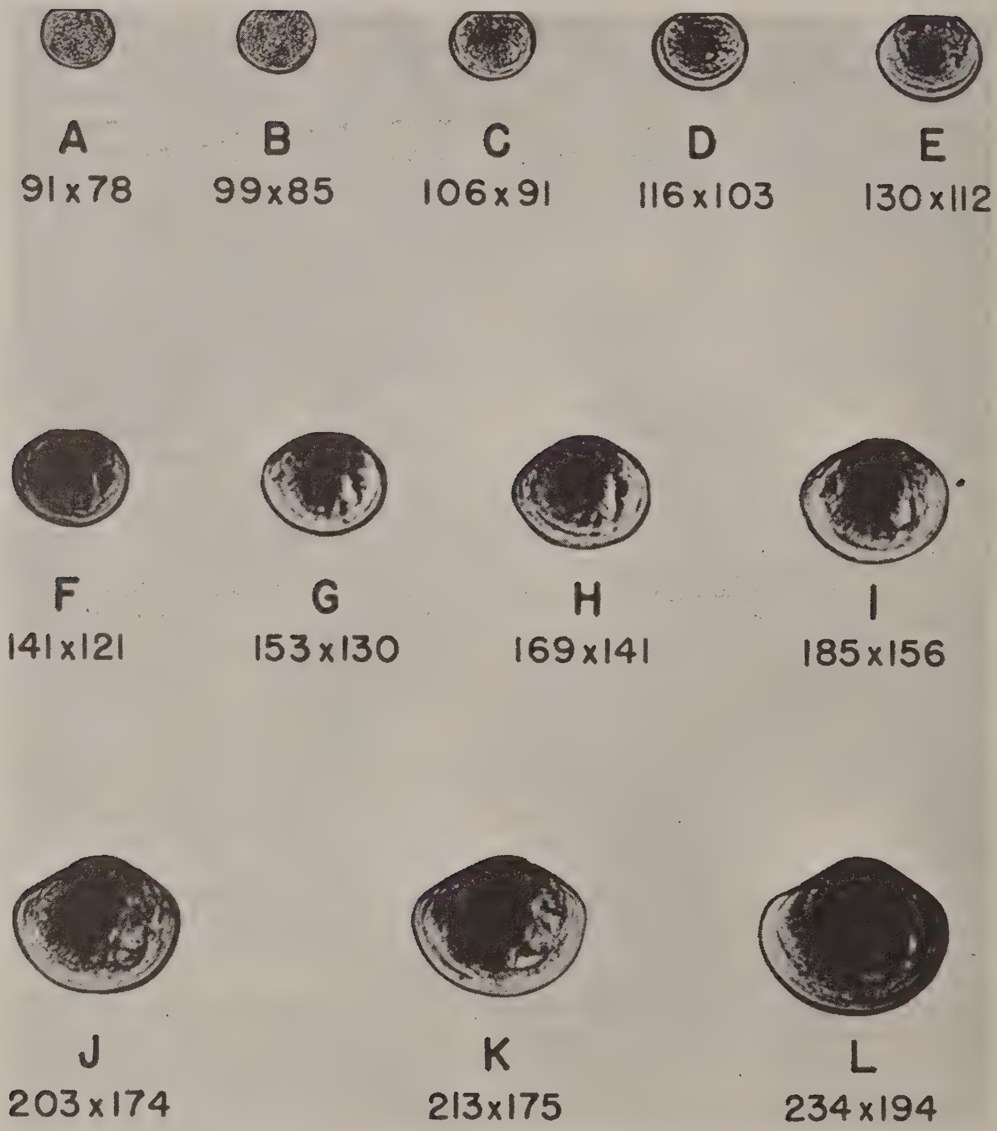
Some larvae already displayed a well-developed foot when only about 205 μ long. Several entirely metamorphosed individuals, with well-developed gills and syphons, were only 220 μ long. On the other hand, some larvae measuring 245 μ in length and with an apparently normal velum were still swimming. The largest swimming larva in our cultures was about 250 x 220 μ.

Sullivan (1948) stated for a related species, *Cardium pinnulatum*, that the size of larvae ranged from 90 x 80 μ, at the earliest straight-hinge stage, to 250 x 230 μ at metamorphosis. Her measurements of *C. pinnulatum*, therefore, closely resembled ours of *L. mortoni*. Jørgensen (1946) found that the larvae of *C. edule* metamorphosed at the size of about 275 to 335 μ, *i.e.* when considerably larger than the larvae of *L. mortoni* or *C. pinnulatum*. He found the larvae of *C. edule* extremely variable in the size at which they reached metamorphosis, a condition that agrees closely with our own observations on *L. mortoni* and the larvae of the majority of other species we reared.

Jørgensen offered a number of references on the studies of larvae of Cardidae in European waters. In his discussion of the sizes of the larvae of different species he mentions that *Cardium echinatum* reached about 480 μ at metamorphosis. The prodissoconch of young bottom stages of another species, *C. minimum*, measured between 330 and 400 μ and averaged approximately 365 μ. In another form, *C. fasciatum*, the largest stages in the plankton were about 300 μ long. Thus, all 3 of the above-mentioned species exceeded the maximum sizes of the larvae of *L. mortoni* in our cultures and the larvae of *C. pinnulatum* described by Sullivan, by at least 50 μ.

In still another species mentioned by Jørgensen, *Cardium exiguum*, metamorphosis appears possible at the length of only 250 μ, a size closely similar to ours. Nothing is known, however, about the possible variations in length of larvae of *C. exiguum* at the time of metamorphosis.

Rees' (1950) description of the larvae of Cardidae pointed out large differences among the larvae of the genus *Cardium*, although he maintained that they conform to a basic type. We cannot agree with the latter conclusion after examining the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G
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H
169x141
I
185x156
J
203x174
K
213x175
L
234x194

FIG. 60. Photographs of larvae of *Laevicardium mortoni* in different stages of development from early straight-hinge stage (A) to the stage of metamorphosis (L). Measurements are in microns; the first figure under a photograph indicates length, and the second, width of the larva.

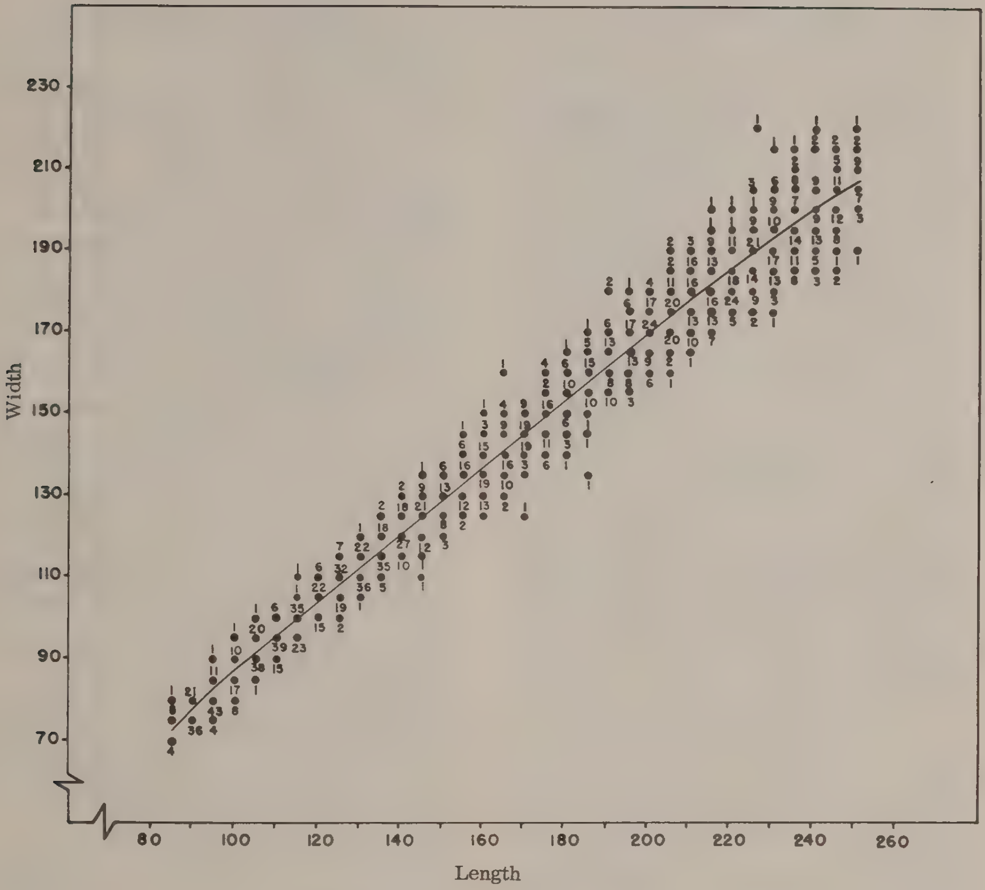

FIG. 61. Length-width relations of larvae of *Laevicardium mortoni* during the entire free-swimming veliger stage. Measurements in microns. The figures at dots indicate the numbers of larvae of each dimension.

photomicrographs he published. Length-width measurements of this group also ran counter to his views.

If the maximum sizes of the larvae of different species of the family Cardidae differ so much, the above observations may be oı considerable biological interest. No final conclusions regarding the matter can be formed, however, until the larvae of all the species of Cardidae discussed have been grown under identical laboratory conditions, where accurate observations can be made on their growth and minimum and maximum sizes. We emphasize, nevertheless, that during our long and varied studies we found that the minimum and maximum sizes of the larvae of closely related species of the same genus, for example, *Crassostrea virginica* and *C. gigas*, or *Ostrea edulis* and *O. lurida*, closely resemble each other.

ACKNOWLEDGMENTS

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RESUMEN

DIMENSIONES Y FORMAS LARVALES DE ALGUNOS BIVALVOS MARINOS

Métodos de reciente desarrollo para la ciranza de larvas de Bivalvos bajo condiciones controladas, ha hecho posible el cultivo de las siguientes especies: *Arca transversa, Mytilus edulis, Modiolus demissus, Anomia simplex, Aequipecten irradians, Ostrea edulis, Ostrea lurida, Crassostrea virginica, Crassostrea gigas, Mercenaria (=Venus) mercenaria, Mercenaria (=Venus) campechiensis, Mulinia lateralis, Tapes semidecussata, Pitar (=Callocardia) morrhuana, Petricola pholadiformis, Ensis directus, Mactra (=Spisula) solidissima, Mya arenaria, Teredo navilis, Laevi-*

cardium mortoni. Estas formas pasaron metamorfosis desde huevos o larvas de recien eclosión, de progenitores conocidos. Una serie de microfotografias y medidas de longitud-diámetro de las larvas, desde temprano estado hasta metamorfosis, se dan para cada especie. Agréganse descripciones de la forma general, prominencia de los umbones y otros caracteres morfológicos de las conchillas larvales durante el crecimento. Se discuten problemas y dificultades en la identificación, especialmente de formas muy relacionadas entre sí, ofreciendo sugestiones para el mejoramiento de los métodos de identificación.

АБСТРАКТ

РАЗМЕРЫ И ФОРМА ЛИЧИНОК НЕКОТОРЫХ МОРСКИХ ДВУСТВОРЧАТЫХ МОЛЛЮСКОВ

Виктор Л. Лозанов, Гарри С. Дейвис и Павел Е. Чанлей

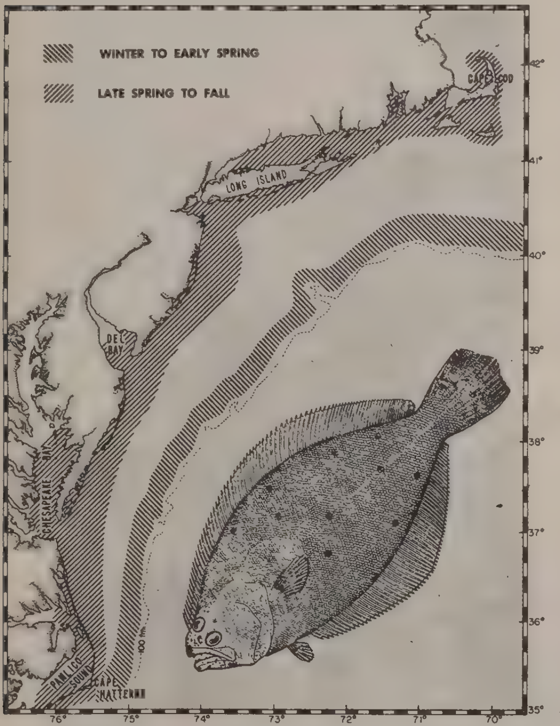
Последние усовершенствования методов выращивания личинок двустворчатых моллюсков в услоьиях лабораторного контроля, дали возможность вырастить культуры следующих 20 видов: *Arca transversa, Mytilus edulis, Modiolus demissus, Anomia simplex, Aequipecten irradians, Ostrea edulis, Ostrea lurida, Crassostrea virginica, Crassostrea gigas, Mercenaria mercenaria, Mercenaria campechiensis, Mulinia lateralis, Tapes semidecussata, Pitar morrhuana, Petricola pholadiformis, Ensis directus, Spisula solidissima, Mya arenaria, Teredo navalis, Laevicardium mortoni.*

Эти виды были вырощены в стадиях после превращения личинки из яйца или же являлись личинками извесных родителей. Для каждого вида даны серии микрофотографических снимков и размеры длины и ширины его личинок. Дополнительно к этим признакам, описаны общие формы, степень выпуклости верхушки и другие морфологические особенности личинковой раковины в процессе ее развития. Обсуждены проблемы и затруднения при определении видов, особенно среди родственных форм, и предложены методы для его улучшения.

SUMMER FLOUNDER ... THE MIDDLE ATLANTIC FLATFISH

The Summer Flounder, or Fluke, *Paralichthys dentatus,* lives in Atlantic coastal waters from New England to northern Florida. This fine table fish is most abundant in the Middle Atlantic Bight, the shallow coastal area between Cape Cod and Cape Hatteras. There it lives on the bottom, close inshore in the shallow waters of bays, sounds, and along open coasts in the summer and offshore in deeper water, largely at depths of 30 to 85 fathoms in winter.

DISTRIBUTION OF SUMMER FLOUNDER IN THE MIDDLE ATLANTIC BIGHT



A Left-handed Flatfish

The Summer Flounder can usually be identified by its color and other characters. It is left-handed: both of its eyes are on its colored, left-hand side, and it lies on the bottom on its right-hand, white side. Color and color pattern are variable for they closely match the color and character of the bottom on which the flounder lies. The left side, however, is usually some shade of brown, gray, or olive with small, round, dark spots, sometimes white-bordered, scattered over it. Fish on light-colored bottom may also have pale-colored, irregularly shaped spots. Small fish are best described as mottled and usually have three dark spots arranged in a triangle on the posterior half of the body. The mouth is large and well armed with sharp teeth. The upper jaw extends back as far as the posterior margin of the left eye. The end of the tail is not simply rounded, as might appear at first glance, but has a rounded tip in the center.

Caught by Commercial and Sport Fishermen

Summer Flounder are caught throughout the year. When the flounders are inshore between late spring and early autumn they are caught mainly by anglers, and commercial fishermen with otter trawls. A few are also caught in commercial traps and seines.

In the winter and early spring otter trawlers catch them on the offshore grounds from south of Cape Cod to off Cape Hatteras. The commercial catch, most of which comes from offshore grounds, has been as high as 20 million pounds annually, although it has decreased in recent years. The 1963 catch was worth $2.8 million to commercial fishermen.

The sport fishery also is of great importance, although precise figures on the sport catch of Summer Flounder are not available. It is likely that the catch of the sport fishery in some States equals or exceeds that of the commercial fishery for this species. Information from surveys in New York, for example, indicates that the catch of Summer Flounder by anglers each summer in the Great South Bay, Long Island, area reaches 1.8

MARINE RESOURCES OF THE ATLANTIC COAST

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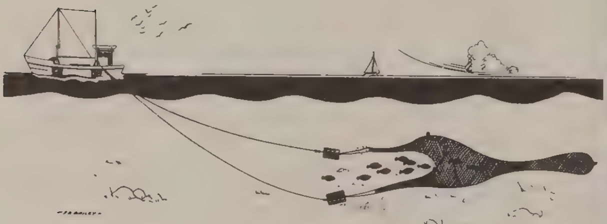
ATLANTIC STATES MARINE FISHERIES COMMISSION, 336 East College Avenue, Tallahassee, Florida 32301

Large numbers of Summer Flounders have been tagged in New York waters to estimate exploitation rates (upper left: *New York Journal-American photo)*. Flounders tagged on a large research vessel are chuted into the sea (upper right: *U. S. Fish and Wildlife Service photo)*. The drawing depicts an otter trawl of the kind used to catch Summer Flounder and other bottom fish; large wooden doors hold the mouth of the net open. These doors are the first out of the water when the net is pulled in (middle right: *New York Journal-American photo)*. This small New England otter trawler is typical of the kind that fishes Summer Flounder on inshore grounds (lower left: *U. S. Fish and Wildlife Service photo)*. The Summer Flounder is popular also as a sport fish — a good catch from an open boat out of Captree State Park docks (lower right: *Long Island State Park Commission photo)*.



PEN
BOAT
SAILS
DAILY
CAPT. JOSEPH II

million fish. In New Jersey, where large numbers of Summer Flounder were tagged along the coast, sportsmen took 40 percent of the recaptured fish.

An Autumn Spawner

Summer Flounder spawn from late September through December during the annual migration from inshore to offshore grounds. Some fish as small as 14 inches long are mature. Mature fish have been caught on grounds off New Jersey in October, eggs taken from them and fertilized, and the young hatched and reared for as long as 12 days after hatching.

Undergoes Typical Flatfish Metamorphosis

The pelagic eggs of the Summer Flounder hatch into larvae that are symmetrical with respect to location of eyes and coloration. As development proceeds, the larvae gradually change in form to the asymmetrical adult form, which has both eyes on the left side of the head. Only the left or eyed side remains colored; the lower, blind side becomes white. This "metamorphosis" is complete by the time the fish is 1 inch long.

Early Stages Drift About

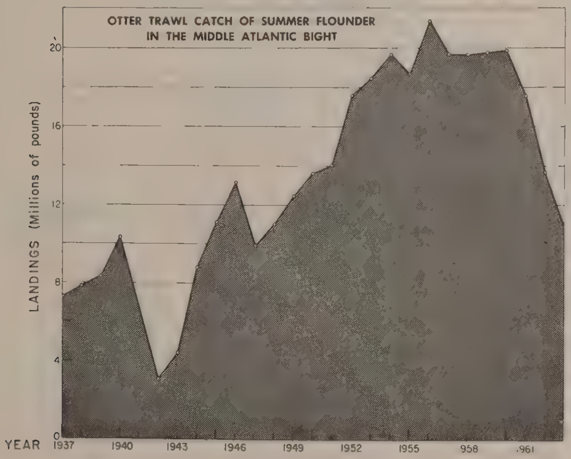
Both the eggs and newly hatched larvae drift passively with the ocean currents. Currents near shore in the central part of the Middle Atlantic Bight flow southward and shoreward in the spawning season. They apparently sweep the eggs and larvae toward bays and sounds along the coast, particularly in the southern part of the Bight where most pelagic stages of the Summer Flounder have been collected. Large numbers of larvae have been caught in fine-mesh plankton nets in bays around Cape Hatteras. Numbers of larvae collected in bays north of Cape Hatteras decrease as one goes northward.

Young up to ¾-inch long have been caught above the bottom in plankton nets in the autumn and winter, and fish as small as 1 inch have been seined on the bottom in the spring. From these observations, it appears that the pelagic life ends in late winter, following the autumn spawning. The fish is then about three-quarters of an inch long. The Flounder then spends the remainder of its life on the bottom.

Northern And Inshore-Offshore Migrations

Young Summer Flounder, less than 10 inches long, are common in the estuaries, bays, and sounds in the southern part of the Middle Atlantic Bight. They are less common at more northerly locations and have not been reported as far north as Cape Cod. Scarcity of small flounders in the north indicates that their principal nursery areas, from the time they become bottom-dwelling until they are about 10 inches long, are the sheltered coastal waters in the southern part of the Bight. As the fish grow larger, some of them probably move northward to maintain the population in the northern part of the Bight.

Tagging studies between New Jersey and Cape Cod, on both inshore and offshore grounds, have shown the pattern of seasonal inshore-offshore migrations. They also have indicated that Summer Flounder that have taken up residence in the northern half of the Bight are unlikely to move in later years to inshore waters south of this area.



A Fast Grower

Summer Flounder growth, as shown by annual rings on ear stones, is rapid — females are 11 inches long when 1 year old; 15 inches at 2 years; 18 inches at 3 years; and 21 inches at 4 years. Males grow more slowly and reach a length of 10 inches at 1 year; 13 inches at 2 years; and 15 inches at 3 years. The growth rate of older fish has not been traced.

A 15-inch fish weighs about 1 pound; a 20-incher, 3 pounds; and a 30-incher, 12 pounds. Fish weighing 30 pounds have been reported, — this probably is the maximum size.

A Strong Predator

This flounder is a strong and active swimmer, and its quick movements and large mouth with strong teeth enable it to catch swiftly moving animals, which it sometimes pursues to the surface of the sea. It feeds largely on fish, squid, shrimp and other crustaceans, and sea worms.

States Are Studying Biology

Recent studies of Summer Flounder have concentrated on fish in the Middle Atlantic Bight. The aims of these studies are to: (1) learn the maturation cycle and define spawning areas; (2) describe egg and larval stages so that their distribution can be determined; (3) work out the distribution and areas of abundance of young-of-the-year; (4) determine the origin of Summer Flounder in the northern part of the Bight and define the limits of migrations; (5) calculate growth rates and age compositions of the stocks; and (6) measure rates of fishing mortality in the sport fishery.

How Maintain This Resource?

The Summer Flounder population of the Middle Atlantic Bight forms a valuable resource that is harvested intensively by both sport and commercial fishermen. As the population of the country grows, the fishing effort will increase further. In the past few years the commercial catch has decreased markedly. At the same time fishermen in some areas have complained of decreasing size of Summer Flounder in their catches, a sign of a high fishing rate. Although landings alone do not necessarily reflect the level of abundance, the sharpness of the decline in catch provides sufficient reason for taking a more serious look at this fishery. Is the resource being overfished? And, if so, how can we use it in a more efficient way?

Before these questions can be answered much more must be learned. The relationship of Summer Flounders in the northern and southern parts of the Bight must be determined. An accurate measure of abundance is required. Estimates of the annual additions of young fish to the populations are needed. More information on the growth rates and age compositions must be obtained, and death rates from natural causes and from fishing activities mut be known.

Recommendation For Studies.

In pursuit of these long-term goals, the Subcommittee for Fisheries of the Atlantic Bight of the ASMFC has recommended that three Summer Flounder cooperative programs be undertaken:

1) Racial studies to define populations. (This project is now underway.)
2) Studies of the distribution of larvae, postlarvae, and young-of-the-year. (A limited program has begun; more funds and personnel are needed.)
3) Studies of the movements of immature Summer Flounder. (These studies are being planned. Fish as small as 6 inches long are to be tagged, particularly in the southern part of the Bight. Results of such tagging are needed to determine conclusively whether small fish from the south, through northward dispersal, contribute significantly to stocks in the north.)

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